

AN ABSTRACT OF THE DISSERTATION OF

Claire M. Tortorelli for the degree of Doctor of Philosophy in Forest Ecosystems and Society presented on May 10, 2022.

Title: Drivers and Impacts of a Recent Annual Grass Invasion: *Ventenata dubia* and Fire in the Inland Northwest

Abstract approved:

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Biological invasions threaten native biodiversity, alter ecosystem function, and are a major cause of economic losses across the planet. The most impactful invaders alter disturbance regimes and initiate state shifts to outside the historical range of variability of the ecosystem. Concern for ecological and economic losses has prompted a rapid expansion of invasion ecology research. However, the continual arrival of new invaders with unknown ecological impacts demands further research to help close the ever-growing knowledge gap. In the Pacific Northwest, a recently introduced, rapidly spreading Eurasian annual grass, *Ventenata dubia* (ventenata) is poised to alter fire behavior and ecosystem function across forest-mosaic landscapes of the Inland Northwest, USA. This dissertation aims to: **1)** determine the biotic and abiotic factors associated with the *V. dubia* invasion, **2)** characterize the relationship between invasion and plant community diversity in burned and unburned areas, **3)** examine how biotic and environmental factors interact to influence community invasion resistance, and **4)** evaluate the influence of *V. dubia* on fuel characteristics and fire behavior at multiple scales.

I used field data, statistical analyses, and landscape fire simulations to determine the drivers and impacts of the *V. dubia* invasion at community and landscape-scales in the Blue Mountains Ecoregion of the Inland Northwest. In Chapter 2, I identified *V. dubia*'s unique niche in forested ecosystems of the region, including historically invasion and fire-resistant dwarf shrublands imbedded within the larger forested landscape. I demonstrated that *V. dubia* expands invasion impacts in these ecosystems rather than occurring in areas already impacted by other invasive annual grasses (*Bromus tectorum* and *Taeniatherum caput-medusae*), increasing the overall invasion footprint. Chapter 2 also examined the relationship between *V. dubia* and plant community diversity with and without fire. I found that *V. dubia* was weakly related to community diversity in unburned areas but was strongly negatively related to diversity and abundance of functionally similar species in burned areas. These results suggest that *V. dubia* may fill an otherwise seemingly unoccupied niche in unburned areas but may outcompete functionally similar species for post-fire resources.

In Chapter 3, I explored interacting drivers of community invasion resistance using an *in-situ* manipulation experiment across three vegetation types. I found that community biomass and some traits (specific leaf area, fine-to-total root volume, and height) may confer invasion resistance of existing communities to *V. dubia*. However, this was only the case in the most productive wet meadow vegetation types. I found no evidence that biomass or community trait composition contributed to invasion resistance in less productive and more stressful low sage-steppe or scab-flat vegetation types, indicating that environmental and biotic factors interact to influence invasion resistance. To assess the potential influence of *V. dubia* invasion on fire behavior across the region, I evaluated the influence of *V. dubia* on fuels and fire in Chapter 4 using a novel application of the landscape-scale Large Fire Simulator, FSim. I show that invasion

increased fire spread, burn probabilities, and fire intensity across forest-mosaic landscapes by increasing fuels and fire occurrence in invaded non-forested areas adjacent to fuel rich forests.

Overall, this dissertation provides some of the first documentation of *V. dubia*'s niche and invasion dynamics in forested landscapes, and characterizes how this invasion differs from other problematic species in this region. My work demonstrates that *V. dubia* may initiate a grass-fire cycle in historically fire- and invasion-resistant scrubland ecosystems and that annual grass invasion can have substantial impacts on fire behavior in uninvaded forests – ecosystems thought to be resistant to annual grass impacts. Together, these chapters provide valuable information from the invasion front to aid the management of this rapidly spreading species.

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Drivers and Impacts of a Recent Annual Grass Invasion: *Ventenata dubia* and Fire in the Inland Northwest

by

Claire M. Tortorelli

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Claire M. Tortorelli, Author

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## CONTRIBUTION OF AUTHORS

In Chapter 2 and 3, Claire M. Tortorelli participated in study/experimental design, data collection, data analysis, and writing of the manuscript. Dr. Meg Krawchuk and Dr. Becky Kerns participated in the study design and writing of the manuscript.

For Chapter 4, Claire M. Tortorelli contributed to the study design, data analysis, and writing of the manuscript. John B. Kim, Alex Dye, Kevin C. Vogler, and Rebecca Lemons participated in the fire modeling. All authors, including Nicole M. Vaillant, Karin Riley, Ty C. Nietupski, Michelle Day, Meg A. Krawchuk, and Becky K. Kerns contributed to the study design and writing of the manuscript.

## TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1 INTRODUCTION .....	1
1.1 GENERAL INTRODUCTION .....	1
1.2 CHAPTER OVERVIEWS .....	5
1.3 FIGURES .....	7
1.4 REFERENCES .....	9
CHAPTER 2 EXPANDING THE INVASION FOOTPRINT: <i>VENTENATA DUBIA</i> AND RELATIONSHIPS TO WILDFIRE, ENVIRONMENT, AND PLANT COMMUNITIES IN THE BLUE MOUNTAINS OF THE INLAND NORTHWEST, USA .....	12
ABSTRACT .....	13
2.1 INTRODUCTION .....	15
2.2 METHODS .....	18
2.2.1 <i>Study Area</i> .....	18
2.2.2 <i>Data acquisition</i> .....	19
2.3 ANALYSIS .....	22
2.3.1 <i>Ventenata dubia</i> habitat characteristics .....	22
2.3.2 <i>Plant communities, invasion intensity, and fire</i> .....	23
2.4 RESULTS .....	25
2.4.1 <i>Ventenata dubia</i> habitat characteristics .....	25
2.4.2 <i>Plant communities, invasion intensity, and fire</i> .....	26
2.5 DISCUSSION .....	27
2.5.1 <i>Ventenata dubia</i> expands invasion footprint .....	27
2.5.2 <i>Burning intensified negative V. dubia-community diversity relationships</i> .....	29
2.5.3 <i>Management implications</i> .....	32
2.6 ACKNOWLEDGMENTS AND DATA .....	34
2.7 REFERENCES .....	34
2.8 FIGURES .....	40
2.9 TABLES .....	47
CHAPTER 3 COMMUNITY INVASION RESISTANCE IS INFLUENCED BY INTERACTIONS BETWEEN PLANT TRAITS AND SITE PRODUCTIVITY .....	52
ABSTRACT .....	53

## TABLE OF CONTENTS (CONTINUED)

	<u>Page</u>
3.1 INTRODUCTION .....	54
3.2 MATERIALS AND METHODS .....	58
3.2.1 <i>Study area</i> .....	58
3.2.2 <i>Vegetation gradient</i> .....	58
3.2.3 <i>Calculating community metrics</i> .....	63
3.3 STATISTICAL ANALYSIS .....	64
3.3.1 <i>Examining species and community traits</i> .....	64
3.3.2 <i>Community traits x vegetation gradient effect on invasion resistance</i> .....	65
3.4 RESULTS .....	66
3.4.1 <i>Comparison of species functional and community traits</i> .....	66
3.4.2 <i>Community metrics x vegetation gradient effect on invasion resistance</i> .....	67
3.5 DISCUSSION .....	68
3.6 ACKNOWLEDGMENTS AND DATA.....	73
3.7 REFERENCES .....	74
3.8 FIGURES .....	78
3.9 TABLES .....	82
 CHAPTER 4 FEEDING THE FIRE: ANNUAL GRASS INVASION FACILITATES SIMULATED FIRE SPREAD ACROSS AN INLAND NORTHWEST FOREST-MOSAIC LANDSCAPE .....	 84
ABSTRACT .....	85
4.1 INTRODUCTION .....	86
4.2 MATERIALS AND METHODS .....	89
4.2.1 <i>Study area</i> .....	89
4.2.2 <i>Fuel characterization: creating custom landscapes</i> .....	90
4.2.3 <i>Wildfire simulation modeling: the Large Fire Simulator (FSim)</i> .....	92
4.3 DATA ANALYSIS.....	94
4.3.1 <i>Burn metrics: ecoregion scale</i> .....	94
4.3.2 <i>Fire transmission</i> .....	95
4.3.3 <i>Spatial patterns of fire: local forest, patch, and landscape scales</i> .....	96
4.4 RESULTS .....	98
4.4.1 <i>Burn metrics: ecoregion scale</i> .....	98

## TABLE OF CONTENTS (CONTINUED)

	<u>Page</u>
4.4.2 <i>Fire transmission</i> .....	99
4.4.3 <i>Spatial patterns of fire: local forest, patch, and landscape scales</i> .....	99
4.5 DISCUSSION .....	102
4.5.1 <i>Invaded dwarf-shrublands heavily impacted</i> .....	102
4.5.2 <i>Invasion facilitates landscape-scale fire spread</i> .....	103
4.5.3 <i>Management implications</i> .....	106
4.6 CONCLUSIONS .....	109
4.6 ACKNOWLEDGEMENTS.....	109
4.7 REFERENCES .....	110
4.8 FIGURES .....	118
4.9 TABLES .....	120
CHAPTER 5 CONCLUSION.....	130
5.1 REFERENCES .....	133
BIBLIOGRAPHY .....	134
APPENDICES .....	149
APPENDIX A SUPPLEMENTARY MATERIAL FOR CHAPTER 2 .....	150
APPENDIX B SUPPLEMENTARY MATERIAL FOR CHAPTER 3.....	162
APPENDIX C SUPPLEMENTARY MATERIAL FOR CHAPTER 4.....	177

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
Figure 1.1 Blue Mountains Ecoregion study region .....	7
Figure 1.1.2 Heavily invaded forest scabland and invasion in a severely burned dry conifer forest 5 years following fire. ....	8
Figure 2.1 Location of sample plots within and just outside of seven fire perimeters (red polygons) in the Blue Mountains Ecoregion study area in northeastern Oregon, U.S.A. ....	40
Figure 2.2 Ordination of sample plots in species space. ....	41
Figure 2.3 <i>Ventenata dubia</i> invasion in forest scablands and surrounding forest. ....	42
Figure 2.4 <i>Ventenata dubia</i> response to understory foliar cover (excluding <i>V. dubia</i> ; panel A) and canopy cover (panel B) in burned and unburned plots with 95% confidence intervals. ....	43
Figure 2.5 Species richness and Shannon diversity response to <i>V. dubia</i> cover with 95% confidence intervals. ....	44
Figure 2.6 Estimates of the change in functional group cover for a 10% increase in <i>V. dubia</i> cover in burned and unburned plots with 95% confidence intervals. Values above 1.0 indicate an increase and below 1.0 indicate a decrease. ....	45
Figure 2.7 Mean shrub cover in burned plots was less than one third of mean shrub cover in unburned plots (estimated ratio = 0.3; 95% CI 0.2 to 0.5) in plots where <i>V. dubia</i> was present (N = 77). ....	46
Figure 3.1 Three community assembly hypotheses and potential interactions with environmental stress. ....	78
Figure 3.2 Sampled communities were distributed across a productivity and soil moisture gradient consisting of three vegetation types: scab-flats, low sage-steppe, and wet meadows. .....	79
Figure 3.3 Non-metric multidimensional scaling ordination of species in trait space. ....	80
Figure 3.4 <i>Ventenata dubia</i> biomass response to (a) weighted mean dissimilarity, (b) nearest species dissimilarity, and (c) hierarchical distance community trait values and (d) resident biomass across three vegetation types spanning a productivity gradient. ....	81
Figure 4.1 Predicted differences in the spatial arrangement of vegetation and fuels associated with grass invasion can influence landscape-scale fire patterns and behavior. ....	118
Figure 4.2 Vegetation map and photos of Blue Mountains Ecoregion .....	119
Figure 4.3 The sparsely vegetated core habitat layer .....	123
Figure 4.4 Simulated annual burn probability (BP) and conditional probability of burning with flame lengths greater than 1.2m (CBP <sub>&gt;1.2m</sub> ) for the uninvaded simulation and percent difference in fire metrics between the invaded and uninvaded simulations ((invaded – uninvaded)/uninvaded*100). ....	124

## LIST OF FIGURES (CONTINUED)

<u>Figure</u>	<u>Page</u>
Figure 4.5 Probability density plots of annual burn probability and conditional probability of burning at > 1.2 m flame lengths for the uninvaded (black outline) and invaded (orange outline) simulations for each vegetation type. ....	125
Figure 4.6 Percent change in mean annual area burned between the invaded and uninvaded simulations (absolute difference / uninvaded*100) for fires that started within “ignition” vegetation types and spread into “burned” vegetation types. ....	126
Figure 4.7 Results from forest neighborhood analysis .....	127
Figure 4.8 Results from patch size analysis.....	128
Figure 4.9 Results from landscape analysis .....	129

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
Table 2.1 Biophysical settings across which vegetation sampling was conducted .....	47
Table 2.2 Ignition dates, acres burned, elevation range, and number of plots sampled within and within 1km of each fire perimeter.....	48
Table 2.3 Indicator species for plots with greater than 15% <i>Ventenata dubia</i> cover .....	49
Table 2.4 Shannon diversity and species richness response to <i>V. dubia</i> cover .....	50
Table 2.5 Functional group cover response to <i>V. dubia</i> cover: .....	51
Table 3.1 Soil depth, soil moisture availability, mean foliar cover, mean resident biomass, and mean species richness for three vegetation types.....	82
Table 3.2 Trait descriptions and abbreviations. (+) and (-) indicate direction of relationships between trait values and functions.....	83
Table 4.1 Total coverage (ha) of fuel models across the BME for LANDFIRE off-the-shelf data, the uninvaded fuelscape, and the invaded fuelscape that were reassigned based on core ventenata habitat and the ventenata map.....	120
Table 4.2 Within the ventenata core habitat area fuel models were reclassified to represent increased fine fuel loading and fire spread rates in invaded areas within the ventenata core habitat as represented below. ....	121
Table 4.3 Summary of burn metrics for the invaded and uninvaded simulations. All values report the mean for the entire ecoregion including all vegetation types. ....	122

## CHAPTER 1 INTRODUCTION

### 1.1 General Introduction

Biological invasions are considered a leading contributor to global biodiversity loss (Gurevitch and Padilla 2004, WWF 2020). Many of the most impactful plant invaders modify their environments by altering soil stability, hydrology, nutrient availability, litter accumulation, access to light, or disturbance regimes to the detriment of native species (Vitousek 1990, Simberloff and Holle 1999, Levine et al. 2003, Brooks et al. 2004). Invasions that alter the type, extent, and continuity of vegetative fuels can affect landscape-scale fire regimes and drive changes to ecosystem process and community structure (D’Antonio and Vitousek 1992).

Invasive grasses are particularly problematic as they often increase fine fuel accumulation, continuity, and ignitability, leading to more intensive and larger fires in historically fuel-limited ecosystems (Young and Evans 1970, Whisenant 1992, Balch et al. 2013, Fusco et al. 2019). Grasses recover quickly after most fires, increasing the potential for invaded areas to re-burn and initiate positive grass-fire feedbacks known as “grass-fire” cycles (D’Antonio and Vitousek 1992). Such shifts in fire regimes can exclude native vegetation, especially species that recover slowly after fire, and facilitate type conversions from forests or shrubland to grasslands (D’Antonio and Vitousek 1992). While grass-fire cycles are well documented in many historically fuel-limited ecosystems such as with *Bromus tectorum* (cheatgrass) invasion in the North American sagebrush-steppe (D’Antonio and Vitousek 1992, Keeley 2000, Brooks et al. 2004, 2016), little is known about how these species influence fire and ecosystem function in landscapes that evolved with more frequent fire, including temperate dry conifer forests and forest-mosaic ecosystems (Fusco et al. 2019).



In the Inland Northwest of the United States, a relatively recently introduced Eurasian annual grass, *Ventenata dubia* (ventenata), is expanding rapidly into agricultural and natural areas where its economic and ecological impacts are already evident. Similar characteristics between *V. dubia* and other invasive annual grass species, including *B. tectorum*, have heightened concerns surrounding the *V. dubia* invasion and its potential to impact native plant communities and fire regimes. Like other Eurasian invasive annual grasses, namely *B. tectorum* and *Taeniatherum caput-medusa* (medusahead), *V. dubia* typically germinates in the fall or early winter and senesces by early to mid-summer (Wallace et al. 2015). This growth cycle differs from the dominant native vegetation throughout the region and may allow *V. dubia* to outcompete established and regenerating native species and crops for early spring moisture (Wallace et al. 2015), and may shift fuel loads and seasonality to outside the historical range of variability. In some areas, *V. dubia* invasion into agricultural fields reduced commercial timothy hay yields by over 50% (Prather and Steele 2009) and invasion threatened populations of sensitive species including *Silene spaldingii* (Spalding's catchfly), *Pyrrocoma liatrifomis* (Palouse Goldenweed), and *Lepidium papilliferum* (Slickspot Peppergrass) (Hill and Gray 2004).

*Ventenata dubia* may be particularly poised to alter ecosystem processes where it increases fuel loads and continuity in historically sparsely vegetated and fire-resistant dwarf-shrublands and dry meadows (locally known as forest scablands) embedded within forest-mosaic landscapes, such as those of the Blue Mountains Ecoregion in the western U.S.A. This could have severe implications for keystone sagebrush species that evolved without pressure from frequent or widespread fire, as well as for ecosystem function (Johnson and Swanson 2005). Moreover, fire-resistant scabland patches within the forest matrix act as natural fire breaks for the surrounding landscape. Increased fuels in these areas may facilitate landscape-scale fire

spread and invasion spread into previously forested areas (Kerns et al. 2020). The propensity for *V. dubia* invasion to initiate grass-fire cycles in historically fire-resistant vegetation types as well as facilitate invasion spread and type conversions after high severity fire in forests, and the potential for landscape-scale fire spread has made *V. dubia* a species of top management concern for the region.

Invasive species are most easily managed and ecological and economic costs mitigated when caught in early stages of the invasion. Despite its growing dominance in many grassland and shrubland ecosystems of the Inland Northwest, *V. dubia* is thought to be in a relatively early stage of invasion (Jones et al. 2018). Since its original documentation in Spokane County, WA in 1952, *V. dubia* has spread to over eleven states and five Canadian provinces (USDA-NRCS 2019) with a documented spread rate of 1.2 million ha per year in 2002 (Native Invasive Plant Council 2001). This rate of spread does not appear to be slowing (Nietupski 2021). Economic and ecological impacts are likely to intensify as *V. dubia* continues to spread throughout the region; however, predicting and managing areas at high risk for invasion has proved difficult due to the lack of knowledge regarding the drivers of *V. dubia* occurrence and distribution, factors contributing to community invasion resistance, and the influence of *V. dubia* on fire regimes. The research presented in this dissertation arose directly from conversations with land managers to address this knowledge gap.

Resistance and susceptibility to invasion often varies with the composition and structure of the recipient plant community coupled with the abiotic environment. The environment can act as a barrier to invasion if the abiotic conditions of a site are not suitable for the establishment or reproduction of an invasive species (Richardson and Pyšek 2006). Even under suitable

environmental conditions, competition from resident species can reduce resource availability and increase community invasion resistance (Davis et al. 2000). For example, diverse and productive plant communities have been shown to be more resistant to invasion (Elton 1958, Chambers et al. 2014), despite typically being relatively resource rich. Given that environmental tolerances and competitive potential vary by species, it is important to consider how biotic and abiotic factors influence the *V. dubia*, and how these might differ from phenotypically similar invasive annual grasses such as *B. tectorum*. A deeper understanding of *V. dubia*'s ecology will aid the development of species-specific management plans and help curb invasion impacts.

The recent invasion of *V. dubia* into the Blue Mountains Ecoregion of the Inland Northwest, U.S.A provides a novel opportunity to investigate the drivers and impacts of an annual grass invader in a forest-mosaic ecosystem (Fig. 1.1). The objectives of my study were to: **1)** determine the biotic and abiotic factors influencing the *V. dubia* invasion, **2)** characterize the impacts of fire and invasion on native plant communities, **3)** examine how biotic and environmental factors interact to influence community invasion resistance, and **4)** evaluate the influence of *V. dubia* on fuel characteristics and fire behavior at community to landscape-scales. This study leverages the early stages of the *V. dubia* invasion to explore the relative influence of biotic and abiotic factors in determining community resistance to *V. dubia* and further develop invasion and community assembly theory. The information gleaned from this study will help land managers target areas at high risk for invasion for preventative treatment and design effective restoration practices in invaded communities to conserve and restore native diversity and ecosystem function.

## 1.2 Chapter overviews

In Chapter 2, I led a study to characterize the environmental niche of *V. dubia* and plant communities associated with invasion and investigate how these differed from two other invasive annual grasses, *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead). Additionally, I evaluated the relationship between plant community diversity and *V. dubia* with and without fire in different environmental contexts. I measured vegetation and site variables at 55 burned and 55 unburned plots from seven recent wildfires spanning the Blue Mountains Ecoregion and characterized the environmental variables and plant community composition and structure associated with the *V. dubia* invasion and other invasive annual grasses. Given recent reports of *V. dubia* expanding into historically uninvaded forest scablands, I expected to find slightly different environmental conditions and plant communities associated with the *V. dubia* invasion compared to the other two annual grasses. Additionally, I expected communities with higher diversity to be more resistant to invasion, since more diverse communities are commonly assumed to have fewer unfilled niches and therefore lower resource availability (Elton 1958, Davis et al. 2000). Classifying the abiotic and biotic drivers of community composition and structure associated with the *V. dubia* invasion can help aid the development of species-specific management approaches and prioritize communities at high risk of resource loss for management.

Chapter 3 further investigates factors influencing invasion by examining how plant community trait composition contributes to invasion resistance, and how these relationships vary along a vegetative productivity gradient. To test this question, I designed a field manipulative experiment where I seeded *V. dubia* into plant communities with varying trait compositions across three vegetation types decreasing in vegetative productivity and perceived moisture

availability: wet meadows, low sage-steppe, and scab-flats. I expected communities composed of species with either (1) more similar trait values to *V. dubia* or (2) traits that conferred greater competitive potential, to have greater resistance to invasion according to contrasting ecological theories (MacArthur and Levins 1967, Thuiller et al. 2010, Price and Pärtel 2013, Gallien et al. 2014). I predicted that competition between species would be strongest in vegetation types with more resource availability (wet meadows), and that these relationships may become weaker, or even shift to facilitative in more stressful environments (e.g. scab-flats) if resident species ameliorate harsh abiotic conditions as posited by the stress-gradient hypothesis (Bertness and Callaway 1994).

In Chapter 4, I examined the influence of *V. dubia* on fire occurrence and behavior across the Blue Mountains Ecoregion using a simulation approach with the Large Fire Simulator (FSim). I compared burn probability, fire transmission, and intensity between the ecoregion with and without invasion by modifying fuels in invaded areas to represent increased spread-rates and flame-lengths based on field observations, fire models, and expert opinion. I expected invasion to have the strongest impact on fire in historically fire-resistant and fuel limited dwarf-shrublands, where higher fuel loads and continuity from the invasion could facilitate increased fire occurrence, spread rates, and intensity. Invasion may also influence fire in dry conifer forests by transmitting fire between forest and non-forested areas, resulting in increased landscape-scale fire occurrence and intensity and compounding widespread concerns about uncharacteristic levels of high severity fire in dry conifer forests (Kerns et al. 2020, Hagmann et al. 2021). Higher fire spread rates and flame lengths as a result of invasion could increase the personnel and equipment resources required to control fires in invaded and adjacent forested areas, complicating regional to global fire management efforts.

### 1.3 Figures



**Figure 1.1** Blue Mountains Ecoregion (BME) study region as defined by the EPA Level III Ecoregions is outlined in blue (Omernik and Griffith 2014).



**Figure 1.1.2** Heavily invaded forest scabland (left) and invasion in a severely burned dry conifer forest (right) 5 years following fire.

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**CHAPTER 2**  
**EXPANDING THE INVASION FOOTPRINT: *VENTENATA DUBIA* AND RELATIONSHIPS TO WILDFIRE,**  
**ENVIRONMENT, AND PLANT COMMUNITIES IN THE BLUE MOUNTAINS OF THE INLAND**  
**NORTHWEST, USA**

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## Abstract

**Questions:** A recently introduced non-native annual grass, *Ventenata dubia*, is challenging previous conceptions of community resistance in dry forest mosaic communities in the Inland Northwest. However, little is known of the drivers and potential ecological impacts of this rapidly expanding species. Here we (1) identify abiotic and biotic habitat characteristics associated with the *V. dubia* invasion and examine how these differ between *V. dubia* and other problematic non-native annual grasses, *Bromus tectorum* and *Taeniatherum caput-medusae*; and (2) determine how burning influences relationships between *V. dubia* and plant community composition and structure to address potential impacts on Inland Northwest dry forest mosaic communities.

**Location:** Blue Mountains Ecoregion of the Inland Northwest, USA

**Methods:** We measured environmental and plant community characteristics in 110 recently burned and nearby unburned plots. Plots were stratified to capture a range of *V. dubia* cover, elevations, biophysical classes, and fire severity. We investigated relationships between *V. dubia*, wildfire, environmental, and plant community characteristics using non-metric multidimensional scaling and linear regressions.

**Results:** *Ventenata dubia* was most abundant in sparsely vegetated, basalt-derived rocky scablands interspersed throughout the forested landscape. Plant communities most heavily invaded by *V. dubia* were largely uninvaded by other non-native annual grasses. *Ventenata dubia* was abundant in both unburned and burned areas, but negative relationships between *V. dubia* cover and community diversity were stronger in burned plots, where keystone sagebrush species were largely absent after fire.

**Conclusions:** *Ventenata dubia* is expanding the overall invasion footprint into previously uninvaded communities. Burning may exacerbate negative relationships between *V. dubia* and species richness, evenness, and functional diversity, especially in communities that historically rarely burned. Understanding the drivers and impacts of the *V. dubia* invasion and recognizing how these differ from other annual grass invasions may provide insight into mechanisms of community invasibility, grass-fire feedbacks, and aid the development of species-specific management plans.

## 2.1 Introduction

Over the past century, non-native annual grass invasions have transformed the American West. Throughout much of the Great Basin, Southwestern deserts, and Californian Mediterranean regions, non-native annual grasses have initiated grass-fire cycles that have converted invaded shrublands to annual grasslands, altering community dynamics, hydrologic and nutrient cycling, reducing livestock forage, and increasing fire frequency and extent (Brooks et al., 2016, 2004; D'Antonio & Vitousek, 1992; Fusco et al., 2019; Mack, 1981). In contrast, many Inland Northwest shrublands and forests remain relatively unaffected by annual grass invasion (Brooks et al., 2016, Chambers, Roundy, Blank, Meyer, & Whittaker, 2007; Fusco et al., 2019), despite having been exposed to propagule pressure from nearby invasions for decades (Johnson & Swanson, 2005). However, some historically resistant communities have shown susceptibility to the recently introduced non-native annual grass, *Venttenata dubia* (commonly known as ventenata), challenging previous conceptions of community resistance to annual grass invasion and potentially expanding the grass-fire cycle footprint into Inland Northwestern dry forest mosaic communities (Bansal, James, & Sheley, 2014; Downing et al., 2020; Jones, Norton, & Prather, 2018; Youngblood, Metlen, & Coe, 2006).

Invasion success is heavily driven by the environmental and biotic characteristics of the recipient community, in concert with propagule pressure. Ecosystems with abundant available resources (e.g. soil moisture, nutrients, or sunlight) are often considered more susceptible to invasion than those with low resource availability (Elton 1958, Davis et al. 2000). For example, nutrient-limited serpentine soils in California maintain low abundances of non-native species despite these same species thriving on adjacent non-serpentine soils (McNaughton 1968, Harrison 1999). Alternatively, in productive ecosystems, competition from established species

may reduce net resource availability and increase community resistance to invasion (Davis et al. 2000).

Resistant communities can become susceptible to invasion if disturbance creates opportunity for invaders by reducing competition from resident species and increasing available resources (D'Antonio and Vitousek 1992, Davis et al. 2000, Chambers et al. 2007, 2014). Establishment of annual grasses can increase surface fuel loads and fire activity in their recipient communities, improving conditions for further invasion and generating a positive feedback between invasion and fire (Brooks et al., 2004; Mack & D'Antonio, 1998). A notable example of this exists in the Great Basin of western North America where the non-native annual grass, *Bromus tectorum* (cheatgrass), increases fine fuel accumulation, continuity, and ignitability in invaded sage-steppe ecosystems. *Bromus tectorum* recovers quickly after fire, often generating grass-fire cycles that result in state shifts in invaded and burned communities previously dominated by species that evolved under pressure from low intensity and infrequent or patchy fires and recover more slowly than fast-growing non-native annuals (Balch, Bradley, D'Antonio, & Gómez-Dans, 2013; Young & Evans, 1970).

Since its introduction to eastern Washington state in 1952 (Barkworth et al. 1993), *V. dubia* has spread to ten US states and four Canadian provinces (USDA plants 2020). *Ventenata dubia* is now widespread across Inland Northwest pastures and natural areas and is rapidly expanding into California's Mediterranean shrublands and throughout the Great Basin (Pavek et al. 2011, USDA-NRCS 2019). *Ventenata dubia*, like *B. tectorum*, is a cool-season C3 grass that germinates in the fall, allowing it to take advantage of early spring moisture in the otherwise dry growing season (Wallace et al. 2015). Once established, *V. dubia* grows quickly and senesces in early summer after seed set when soil moisture is depleted. These characteristics, along with *V.*

*dubia*'s high reproductive potential (Wallace et al. 2015), may provide *V. dubia* a competitive advantage over established, native species, especially in historically sparsely vegetated communities that were previously resistant to fire and invasion. However, the extent to which *V. dubia* actively competes with native species, the influence of fire on *V. dubia*'s competitive potential, and the overall impacts of *V. dubia* invasion on community composition and structure remain relatively unexplored.

Invasive species management becomes increasingly challenging as the invasion progresses (Harvey and Mazzotti 2014). It is imperative to develop an understanding of the drivers and impacts of new non-native species in early invasion stages to inform proactive management strategies, aid early detection and rapid response, and curb invasion spread. Although prevalent across many Inland Northwest communities, it is believed that *V. dubia* has not yet met its full invasion potential (Jones, Norton, & Prather, 2018). Here, we use field collections of plant community and site characteristics across the Inland Northwest to (1) identify abiotic and biotic habitat characteristics associated with the *V. dubia* invasion and examine how these drivers might differ between *V. dubia* and other problematic non-native annual grasses in the Inland Northwest, *B. tectorum* and *T. caput-medusae*; and (2) determine how burning influences relationships between *V. dubia* and plant community composition and structure to address potential impacts of the invasion and altered disturbance regimes on Inland Northwest dry forest and shrubland communities.



## **2.2 Methods**

### ***2.2.1 Study Area***

The study was located in the heart of the Inland Northwest, USA, within the Blue Mountains Ecoregion (Fig. 2.1). The Blue Mountains Ecoregion lies in the rain shadow of the Cascade Range, resulting in continental, semiarid climates more typical of the warmer and drier Great Basin. These areas receive on average between 27 and 57 cm (10.6-22.4 in) of precipitation per year (PRISM Climate Group 2019). Precipitation primarily falls between November and June. Average high temperatures are in the mid to upper 20s °C and average low temperatures fall in the -10s °C (Western Regional Climate Center, 2019). However, temperature and precipitation exhibit high spatial variation with higher elevations typically receiving more precipitation and cooler temperatures than lower elevations.

The Blue Mountains Ecoregion functions ecologically and floristically as a transverse bridge between the Cascade Mountains to the west and the Rocky Mountains to the east. Variable topography, wide elevation gradient, and a patchwork of soil types within the region support ecosystems ranging from dry grasslands and shrub-steppe to woodlands and mixed-conifer forests (Anderson, Borman, & Krueger, 1998; Soulard, 2012). Dry conifer forests embedded with patches of sparsely vegetated, rocky dry meadows and dwarf shrublands (“forest scablands”) are prevalent across the landscape. We sampled an elevation and soil moisture gradient spanning a variety of biophysical settings characterized by dominant woody vegetation and structure (Table 2.1).

### 2.2.2 Data acquisition

Field sampling was conducted from May through August 2018 within and adjacent to seven recently burned fire perimeters (from 2014-2017) spanning the Blue Mountains Ecoregion (Fig. 2.1; Table 2.2). Because *V. dubia* had not yet been mapped throughout the study region, our study was designed to maximize the likelihood of finding *V. dubia* according to local experts (USFS botanists). We stratified our sampling to capture a range of *V. dubia* abundance, environmental characteristics, burn severities, and biophysical settings within 1 km of the fire perimeters and limited to federally managed lands. We chose fire perimeters that burned within the last five years on accessible federally managed land, and covered a wide environmental gradient including at least one of our five defined biophysical settings, outlined in Table 2.1. All fire perimeters encompassed more than one biophysical setting, but the range of biophysical settings encompassed varied between fire perimeters and their corresponding elevational gradients. Fire perimeters at lower elevations were sampled in May and June and fire perimeters at higher elevations were sampled in July and August to capture the flora at similar phenological stages throughout the sampling period.

An equal number of “burned” plots (exhibiting visual burn evidence) and “unburned” plots were sampled (N = 110 plots). We attempted to sample unburned and burned plots with similar environmental and community characteristics when possible (Table 2.1). Plots of the same burn status (burned or unburned) were separated by at least 400 m to maintain independence between samples. Burned and unburned plots of similar environmental and community characteristics ranged in separation distance from 50 m to several kilometers. We surveyed a range of biophysical settings within the fire perimeters for *V. dubia* abundance prior to establishing plots and established fewer plots in fire perimeters and biophysical settings where we found little or no

*V. dubia* to focus sampling efforts on fire perimeters and biophysical settings with a wide range of *V. dubia* abundances.

We used a modified version of the USDA nested three-spoke survey approach (Herrick et al. 2017) for field sampling. Data were collected at 110 plots, with each plot consisting of three 30 m transect “spokes”. On each transect, six 50x20 cm quadrats were placed, one every five meters, totaling 330 transects and 1,980 quadrats. In each quadrat, we measured vascular plant foliar cover including *V. dubia* cover and soil surface cover to the nearest 1%, burn evidence (binary: visual char), evidence of grazing (binary), and litter depth (cm). Soil surface categories included cover of bare ground (loose mineral soil), biocrust, moss, rock, gravel, litter, woody litter, and scat. Quadrat level vegetation and soil surface cover and litter depth were averaged up to the plot level for analyses. Burn and grazing evidence were totaled at the plot level for analyses.

Vascular plants that we were unable to identify to species in the field were sampled and identified to the lowest taxonomic group possible using dichotomous keys. Poor quality specimens were recorded by lifeform (e.g. unknown shrub). Vascular plant identifications were confirmed by Richard Halse at Oregon State University (OSU) and vouchers are housed with the Landscape and Conservation Science Research Group at OSU. Nomenclature was recorded following the USDA Plants Database (2019).

We sampled soils from depths of 0-10 cm and 10-20 cm and estimated soil depth from small pits at 5 m along each transect. Samples within each plot were combined by depth for processing and analysis. All soil samples were hand textured and analyzed for pH (Thomas 1996) and organic matter via loss on ignition (Nelson and Sommers 1996). Textures were reported as mean sand, silt, and clay (%) for each texture class (Thien 1979). A subset of 58 plots

were analyzed for phosphorus (Olsen and Sommers 1982) at the OSU Watershed Forest Soils and Central Analytical Laboratories.

We recorded canopy cover, basal area, topography (slope, slope shape, aspect), vegetation and soil disturbance, and fire severity at the plot level. Canopy cover was measured at plot center by averaging spherical densiometer measurements facing each of the four cardinal directions. Basal area was estimated from plot center using a 20 basal area factor prism. Vegetation and soil disturbance were recorded as low (<10% soil and vegetation appear to be physically disturbed by grazing, fire, rodent activity, or human activity), moderate (10-50%), or high (>50%; Seipel, Rew, Taylor, Maxwell, & Lehnhoff, 2018). Plots were categorized by fire severity in the field as low severity or patchy (1-10% of woody vegetation appeared to be killed by fire), moderate severity (>10-50%), or high severity (>50%).

Coarse scale burn severity was also calculated using differenced Normalized Burn Ratios (dNBR). We derived dNBR from 30-meter Landsat TM+ satellite imagery, measured immediately post-fire to improve estimates of burn severity by decreasing the detection of post-fire vegetation recovery. Calculations were made using Google Earth Engine (Gorelick et al., 2017).

We characterized the antecedent climate conditions for the field season and the climatological norms for each plot. Precipitation from January through June 2018, 30-year mean yearly precipitation, mean temperature, and maximum temperature values were extracted from the Parameter-elevation Regressions on Independent Slopes Model database for each plot (PRISM 2018). Heat load and potential direct incident radiation were estimated using metrics from McCune (2007). Distance from nearest road was calculated from plot center using Oregon Department of Transportation roads layer in ArcGIS (ESRI, 2011). Estimates of parent material

were extracted from the “Geology of Oregon” spatial layer in ArcGIS (Ludington et al. 2005, ESRI 2011). All recorded environmental variables are presented in Table A.2.

## 2.3 Analysis

### 2.3.1 *Ventenata dubia* habitat characteristics

To address our first objective, we identified the environmental and community characteristics associated with the *V. dubia* invasion and compared how *V. dubia*’s realized niche differs from the non-native annual grasses *B. tectorum* and *T. caput-medusae* using nonmetric multidimensional scaling (NMS) and indicator species analysis. Cover of each species was square root transformed and rare species that occurred in fewer than 5% of plots were removed from analysis to reduce noise and strengthen the relationship between community composition and environmental variables (N = 132 species; Table A.1). We overlaid the ordination with biplots of environmental variables (Table A.2). Predictor variable vectors increase proportionally according to their linear correlation with the ordination axes (minimum  $R^2 = 0.2$ ). Correlated predictor variables were identified and all but the variable with the highest  $R^2$  values for each axis were removed to improve readability and interpretability of the ordinations (Table A.2).

We superimposed nonlinear response surfaces on the ordination for *B. tectorum*, *T. caput-medusae*, and *V. dubia* using “hilltop” plots. The hilltop plots outline the contour representing the top 20% of each species’ response surface in relation to the ordination axes by interpolating between the existing sample plots. These contours are accompanied by a  $R^2$  measure of fit calculated using the sum of squared differences between observed and estimated values (McCune and Mefford 2011). All NMS analyses were performed using the Bray Curtis

distance measure in the software package PCORD with sample plots ordinated in species space and are rotated to load *V. dubia* on Axis 1 (McCune and Mefford 2011).

We examined *V. dubia* relationships to total understory cover (excluding *V. dubia* cover) and canopy cover in burned and unburned plots using linear mixed effects models with an interaction term for plot level burn status (burned or unburned) and a random effect for fire perimeter. *Ventenata dubia* cover was log transformed to improve model fit.

We used indicator species analysis (ISA) to identify species that were strong indicators for plots with high *V. dubia* cover (Sud et al. 1997). We performed an ISA with our transformed and simplified study matrix for plots with over 15% *V. dubia* cover. This threshold was chosen to reflect plots that were clearly visibly invaded and would likely spread rapidly with favorable conditions. Non-native *Bromus* spp. (excluding *B. tectorum*), including *Bromus arvensis*, *Bromus briziformis*, *Bromus hordeaceus*, *Bromus racemosus*, and *Bromus squarrosus*, were lumped for indicator species analysis as field differentiation is difficult and they are known to hybridize (Knowles 1944). Indicator values were tested for statistical significance using a randomization (Monte Carlo) test with 4999 runs and performed in PCORD (McCune & Mefford, 2011).

### ***2.3.2 Plant communities, invasion intensity, and fire***

To address objective 2, we examined the response of diversity and structure to *V. dubia* cover and burning in invaded communities by modeling Shannon diversity, native and non-native species richness, and foliar cover (%) for six functional groups in response to *V. dubia* cover. Plots where *V. dubia* was absent were removed from these analyses to focus the analyses on invaded aeras (N = 77 plots where *V. dubia* cover > 0). This was done to remove plots that

may be susceptible to invasion but have potentially not yet been exposed to *V. dubia*. Rare species and *V. dubia* were not removed for Shannon diversity and species richness analyses to maintain the full species composition for each plot ( $N = 269$  species). Shannon diversity and species richness response to *V. dubia* were modeled using linear mixed effects models with an interaction term for plot level burned status and a random effect for fire perimeter. To evaluate how mean diversity and species richness differ in plots where *V. dubia* was absent ( $N = 33$ ) and where *V. dubia* was present ( $N = 77$ ), we modeled diversity and species richness response to *V. dubia* presence using linear mixed effects models with an interaction term for *V. dubia* presence and burn status and a random effect for fire perimeter.

For each plot, foliar cover was lumped by functional group: native and non-native annual grasses (excluding *V. dubia*), perennial grasses, native and non-native annual forbs, perennial forbs, all non-native species, and shrubs. Functional groups are often used to describe groups of morphologically similar species accessing similar resources (Grime, 1979). Species reported as both annual and biannual from the USDA Plants Database (2019), were classified as annuals, and species reported as only biannual, or perennial and biannual were classified as perennials. Cover values for all eight functional groups were log-transformed to improve normality. We adjusted one zero value of annual grass cover by adding the square of the first quartile divided by the third quartile (Stahel 2008). Cover of each functional group was modeled using mixed effects models with an interaction term for burn status and a random effect for fire perimeter. Shrub cover was modeled using a Tweedie distribution with a log link to improve the fit of the data with a high proportion of zeros (Tweedie 1984, Jorgensen 1987). We evaluated differences in mean shrub cover between burned and unburned plots with a linear mixed effects model with a

random effect for fire perimeter. All models were conducted in R using the lme4, nlme, and glmmTMB packages (R Core Team, 2018).

## 2.4 Results

### 2.4.1 *Ventenata dubia* habitat characteristics

*Ventenata dubia* and *B. tectorum* hilltop response surfaces were separated in the three-dimensional NMS ordination (stress 14.68), indicating that plant communities differed between plots with high *V. dubia* cover and high *B. tectorum* cover (Fig. 2.2). *Ventenata dubia* was most strongly associated with burned and unburned woodland, dry forest, and forest scabland plots (Fig. 2.2 & 2.3), while *B. tectorum* was most strongly associated with burned woodland and dry forest plots (Fig. 2.2). Environmental variables most strongly correlated with *V. dubia* along Axis 1 included basaltic parent material, total moss cover, low soil phosphorus (P) from 0-10 cm, and low mineral soil cover (bare ground). *Bromus tectorum* was negatively associated with rock cover (%) and basalt and positively correlated with plots with high cover of bare ground and high soil phosphorus along Axis 1 (Fig. 2.2a). Both *V. dubia* and *B. tectorum* were weakly associated with Axis 2 and corresponding environmental variables including increasing tree canopy cover, soil organic carbon measured as loss on ignition (LOI) from 10-20 cm, elevation, and maximum temperature (Tmax). However, the response surfaces separated along Axis 3, where, unlike *V. dubia* which was common in both burned and unburned plots, *B. tectorum* was primarily associated with burned plots and high fire severity (Fig. 2.2b).

*Ventenata dubia* and *T. caput-medusae* displayed overlapping response surfaces. However, *T. caput-medusae* was more strongly correlated with lower elevation forest scabland plots with high maximum temperatures along Axis 2 (Fig. 2.2a) and severely burned forest plots along Axis 3 than *V. dubia* (Fig. 2.2b). Unlike *V. dubia*, *T. caput-medusae* was weakly associated with basalt



and sandstone along Axis 1. *Ventenata dubia* extended into higher elevation unburned forest scabland, woodland, and forest plots with higher canopy and litter cover compared to *T. caput-medusae*.

*Ventenata dubia* heavily invaded plots with a wide range of understory foliar cover and canopy cover (Fig. 2.4). We observed plots with greater than 75% *V. dubia* cover in burned areas when understory foliar cover was less than 50% (Fig. 2.4a) and canopy cover was less than 20% (Fig. 2.4b). *Ventenata dubia* was present in plots with up to 50% canopy cover, and heavily invaded burned and unburned plots (*V. dubia* >30% cover) with up to 45% canopy cover (Fig. 2.4b).

The strongest indicator species for plots with high cover of *V. dubia* were predominantly annual grasses and forbs. Non-native annual bromes (excluding *B. tectorum*) were the strongest indicator followed by three native annual forbs (*Agoseris heterophylla*, *Blepharipappus scaber*, and *Holastium umbellatum*), a non-native annual forb (*Draba verna*), and a shallow-rooted perennial bunchgrass (*Danthonia unispicata*; Table 2.3).

#### **2.4.2 Plant communities, invasion intensity, and fire**

Shannon diversity decreased when *V. dubia* cover increased in both burned and unburned plots (Fig. 2.5a); however, Shannon diversity decreased more strongly with increasing *V. dubia* cover in burned plots than in unburned plots (Table 2.4). Native species richness decreased when *V. dubia* cover increased in burned plots and was variable in response to *V. dubia* cover in unburned plots (Fig. 2.5b; Table 2.4). Non-native species richness had little relationship to *V. dubia* cover in both burned and unburned plots (Fig. 2.5b; Table 2.4). Mean native species richness was greater than non-native species richness regardless of *V. dubia* cover or burn status (Fig. 2.5b). Mean Shannon diversity and native species richness and variances did not strongly

differ between plots where *V. dubia* was absent and where *V. dubia* was present (Fig. A.3). Mean non-native species richness was higher in both burned and unburned plots where *V. dubia* was present than in plots where *V. dubia* was absent (estimates for this difference in richness = 3.1 and 3.2 more species respectively, CIs = 1.5 to 4.7 and 1.7 to 4.7 more species respectively).

Annual forbs, annual grasses, non-native species, perennial forbs, and shrubs were negatively associated with *V. dubia* cover in burned plots (Fig. 2.6). Perennial forbs were the only functional group to be negatively correlated with *V. dubia* in unburned plots (Fig. 2.6). Burning had the greatest effect on functional group cover response to *V. dubia* cover for annual forbs, annual grasses, and non-native species (excluding *V. dubia*; Table 2.5). Shrubs were nearly absent from burned plots (mean shrub cover <2%). Mean shrub cover in burned plots was less than one third of mean shrub cover in unburned plots (Fig. 2.7).

## 2.5 Discussion

Our study characterizes the unique niche invaded by *V. dubia* compared to other non-native annual grasses (*B. tectorum* and *T. caput-medusae*) and demonstrates that *V. dubia* is expanding the grass-invasion footprint into previously resistant Inland Northwest forest mosaic communities. Our results suggest that *V. dubia* heavily invades unburned and burned areas and burning may exacerbate negative relationships between *V. dubia* and diversity, species richness, and community structure, potentially contributing to state-shifts from shrub dominated communities to non-native annual grasslands.

### 2.5.1 *Ventenata dubia* expands invasion footprint

*Ventenata dubia* differed from *B. tectorum* and *T. caput-medusae* by heavily invading both burned and unburned dry forest, woodland, and forest scablands ranging from 1250 m to 1665 m

throughout the Blue Mountains Ecoregion. *Ventenata dubia*'s tolerance for the frigid basalt-derived lithosols characteristic of forest scablands further separated its realized niche from *B. tectorum* and *T. caput-medusae*, increasing the overall invasion footprint. Prior to the *V. dubia* invasion, forest scablands were relatively resistant to invasion impacts despite being exposed to non-native annual grasses for decades (Johnson & Swanson, 2005). Although, *B. tectorum* often germinates in relatively cold temperatures, it experiences limited growth and reproduction under frigid soil temperature regimes (Chambers et al. 2007, Roundy et al. 2007). *Ventenata dubia*'s extremely shallow root system (between 1 and 5 cm) may allow it to take advantage of early spring moisture near the soil surface to thrive in these otherwise moisture limited systems (Wallace et al. 2015). *Ventenata dubia* was also positively associated with rock cover, which can partially mediate the harsh seasonal swings in moisture availability by lowering the evaporation rate (Poesen & Lavee, 1994).

Both dry and moist shrublands showed resistance to *V. dubia* invasion, despite lower-elevation sagebrush-steppe communities within the Inland Northwest and the nearby Great Basin demonstrating high susceptibility to invasion by *B. tectorum* (Chambers et al. 2007). Additionally, neither *B. tectorum* nor *T. caput-medusae* were found to be strong indicators for plots with >15% cover of *V. dubia*. In concordance with our findings, Jones et al. (2018) reported a negative relationship between *V. dubia* and *B. tectorum* abundances in Inland Northwest sagebrush communities, suggesting that this trend may extend outside of our immediate study area. However, as *V. dubia* is still in a relatively early stage of invasion (Jones et al. 2018), it is unknown whether the biotic and abiotic characteristics of these dry and moist shrublands confer an inherent resistance to *V. dubia* invasion, or if increased propagule pressure and residence time will find these areas susceptible.

Although we found *V. dubia* to be associated with a distinct realized niche, it may invade areas currently dominated by other non-native annual grasses under different environmental conditions. We note that our sampling was focused along a gradient of *V. dubia* cover and an unbalanced sample of biophysical classes during one sampling season within the Blue Mountains Ecoregion. We did not aim to characterize the entire environmental range of all annual grasses, nor did we perform a balanced random sample across biophysical settings over multiple years, potentially affecting the representativity of the gradient and limiting our findings to climatic conditions similar to those in summer 2018. For example, Jones et al. (2018) found *T. caput-medusae* to be a strong indicator for *V. dubia* in lower elevation sagebrush-steppe (916-1,662 m) where soils are generally warmer and *T. caput-medusae* is more abundant. Additionally, *V. dubia* was reported replacing non-native annual grasses, including *T. caput-medusa* and *B. tectorum*, in more productive grassland communities within the Inland Northwest (Prather and Burke 2011).

### ***2.5.2 Burning intensified negative V. dubia-community diversity relationships***

*Ventenata dubia* may be in-filling gaps rather than outcompeting resident species in unburned areas. Our findings of Shannon diversity decreasing with increasing *V. dubia* cover indicate that *V. dubia* is shifting the proportional contribution of species to composition. Species richness and cover of annual grasses and forbs did not decrease with *V. dubia* in unburned plots, indicating that *V. dubia* may be in-filling unoccupied gaps and vacant niches surrounding existing species in unburned communities, impacting species evenness rather than competitively excluding species. These results contrast findings of *B. tectorum* preventing establishment of native species and reducing diversity by depleting spring moisture in unburned communities (Cline et al. 1977, Harris 1977) and studies finding non-native annuals to competitively exclude

native annuals from unburned Californian desert communities (Brooks 2000, DeFalco et al. 2003).

Communities with high cover are often more resistant to invasion, in part because the communities are more highly saturated and host fewer available resources (Elton 1958, MacArthur 1970). Our findings show a negative relationship between *V. dubia* and perennial forbs in both burned and unburned plots, suggesting that *V. dubia* may preferentially invade areas with lower cover of established perennial forbs. Compared to findings from the Great Basin, where perennial grasses have been shown to increase community resistance to *B. tectorum* invasion (Booth et al. 2003, Beckstead and Augspurger 2004), we found limited evidence to suggest that perennial grasses confer community resistance to *V. dubia* in the Blue Mountains Ecoregion.

Burning intensified negative relationships between *V. dubia* cover and native species richness, annual forb cover, annual grass cover, and non-native species cover. This finding may suggest that, while not heavily competing with species in unburned areas, *V. dubia* may more efficiently allocate post-fire resources, potentially excluding species from burned areas. This could provide an example of increased priority effects of *V. dubia* in burned areas. In the Great Basin sagebrush-steppe, *B. tectorum* establishes quickly after fires and is known to suppress the recovery of native species by more efficiently allocating and depleting soil resources (Melgoza & Nowak, 1991; Monaco et al., 2003). This is especially impactful for the establishment of seedlings that depend on water availability near the soil surface where competition with annual grasses is greatest (Harris, 1977; Melgoza, Nowak, & Tausch, 1990). For example, post-fire establishment of an obligate-seeding conifer in Australia was found to be heavily impacted by the invasion of the non-native perennial grass *Andropogon gayanus* (gamba grass) in a tropical

savanna (Bowman et al. 2014). Our findings compliment studies from invaded California grasslands and ponderosa pine forests that have found disturbance to be a stronger driver of non-native annual grass dominance than competitive ability or community composition alone (Corbin and D’Antonio 2004, Kerns and Day 2017), and support general invasion frameworks that suggest community invasibility increases following disturbances such as fire (Davis et al. 2000, Chambers et al. 2007).

Alternatively, negative relationships between *V. dubia* and community diversity in burned plots could indicate that increasing species richness and cover of functionally similar annuals may limit *V. dubia* establishment and growth post-fire. Functional similarity between invaders and resident communities has been shown to increase community resistance to invasion, although often more successfully limiting the establishment of invading forbs than grasses (Price and Pärtel, 2013).

Shrubs were largely absent from burned plots with high *V. dubia* cover. This observation was strongly driven by the loss of non-sprouting sagebrush species, *A. rigida* and *A. arbuscula* from burned forest scabland plots. Despite our short observation window, two to four years post fire, we saw no evidence of sagebrush individuals re-establishing to indicate recovery of this important structural component of forest scabland communities. Although *A. tridentata* seeds have been found to survive in the seedbank for up to 5 years post fire, few seeds germinate after the first year (Meyer 2008). Reestablishment after fire is thought to occur very slowly for *A. rigida* and is likely maintained by short-distance dispersal from nearby unburned sagebrush islands acting as fire refugia (Agee, 1994; Steenvoorden et al. 2018). The loss of *A. rigida* and *A. arbuscula* could have broad ecosystem effects. These relatively deep-rooted shrubs improve moisture infiltration into the soil, help prevent erosion, and concentrate soil nutrients creating

fertile “islands” in otherwise nutrient limited systems (Stubbs and Pyke 2005, Allen et al. 2011). *Artemisia rigida* provides important habitat for endangered sage grouse and provides winter forage for elk (Daubenmire, 1970; Tirhi, 1995). Grass-fire cycles in arid and semi-arid shrub-steppe ecosystems have reduced soil fertility and overall ecosystem productivity by removing shrub components (Allen et al. 2011). Burning as a result of the rapid post-fire accumulation of fine fuels could shift historically pyro-resistant forest scablands to annual grasslands, consequently altering hydrologic cycling, soil stability, and habitat quality in these ecosystems.

### **2.5.3 Management implications**

Mitigating large-scale ecological impacts of an invasion are contingent on predicting areas at high risk for invasion, early detection, mitigating spread, and prioritizing treatments (Harvey & Mazzotti, 2014). We identified the environmental and community characters associated with *V. dubia* (including high rock cover and basalt parent material) and indicator species (annual bromes, annual forbs, and *D. unispicata*), which can be used to detect areas at high risk for *V. dubia* invasion across the Blue Mountains Ecoregion and prioritize treatments at early stages in the invasion process when eradication is most likely (Harvey and Mazzotti 2014). Additionally, we characterize how *V. dubia*’s realized niche differs from other annual grasses, aiding the design of effective *V. dubia* specific management plans.

Unlike *B. tectorum* and *T. caput-medusae*, the *V. dubia* invasion is impacting forest scablands interspersed throughout the larger forested landscape rather than within dominantly shrub-steppe ecosystems. Rapid accumulation of *V. dubia* cover post-fire could initiate a positive feedback cycle between *V. dubia* and fire, similar to *B. tectorum* induced grass-fire cycles in the Great Basin (D’Antonio & Vitousek, 1992). Prior to invasion, fuel-limited forest scablands served as natural fire breaks, increasing burn heterogeneity throughout the larger forested

landscape. Increased fine fuel cover in these historically fuel limited communities could allow fire to spread into and between adjacent forests more easily, potentially increasing forest fire activity (Kerns et al., 2020). The increasing loss of forest canopy from stand-replacing fire in these dry forest ecosystems (Odion, Moritz, & DellaSala, 2010; Reilly et al., 2020), and reduced competition from understory species may promote the further expansion of *V. dubia* into recently burned dry mixed-conifer forests, further exacerbating the invasion. Such shifts have the potential to alter landscape-scale disturbance regimes and ecological processes in open and forested ecosystems across the Intermountain West (Kerns et al., 2020).

*Venttenata dubia* invaded readily after wildfires that burned during the summer (between June 29 and August 12) in dry forests and forest scablands, suggesting that summer season prescribed fires alone may not be an effective control strategy for reducing invasion levels. Fire, coupled with *V. dubia* invasion was associated with lower diversity, species richness, and functional group cover, indicating that prescribed fire during the summer season could reduce biodiversity and have negative ecological impacts to invaded communities. This may be especially true in forest scablands where burning coupled with invasion may initiate a state shift from shrub-steppe to annual grasslands. However, the areas that we sampled burned in wildfires with specific weather conditions and may not be representative of plant community or *V. dubia* response to summer prescribed burning under different conditions or burning in other seasons. Further observations and experimentation are necessary to fully understand the ecological impacts of the *V. dubia* invasion. However, our findings may aid managers in developing species specific, early response management plans to mitigate potential impacts, while adding evidence to further develop community invasibility and grass-fire cycle frameworks.



## 2.6 Acknowledgments and Data

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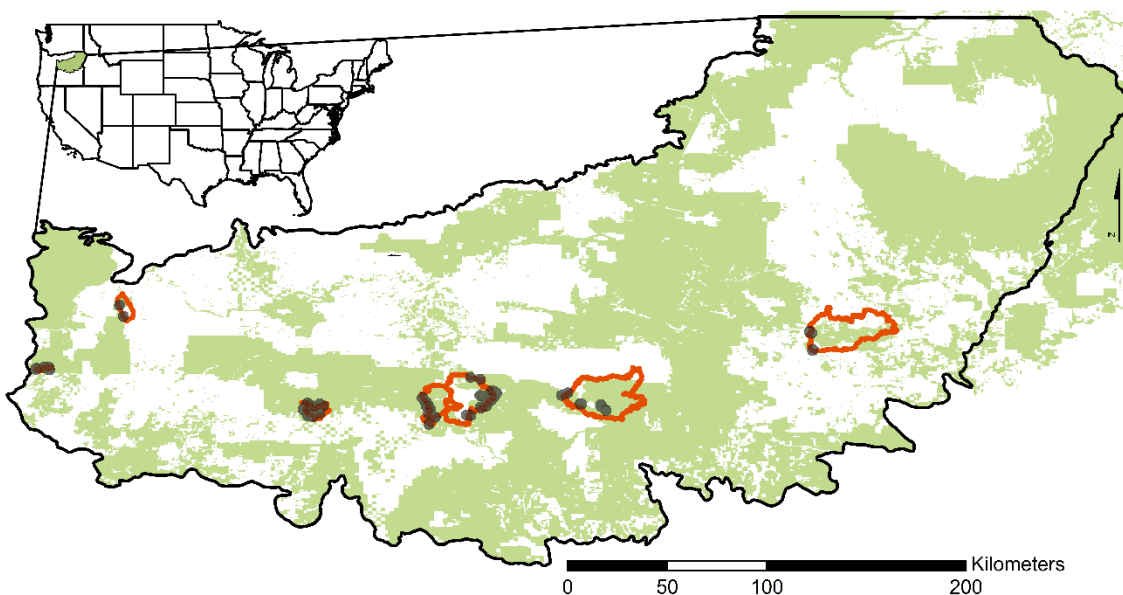
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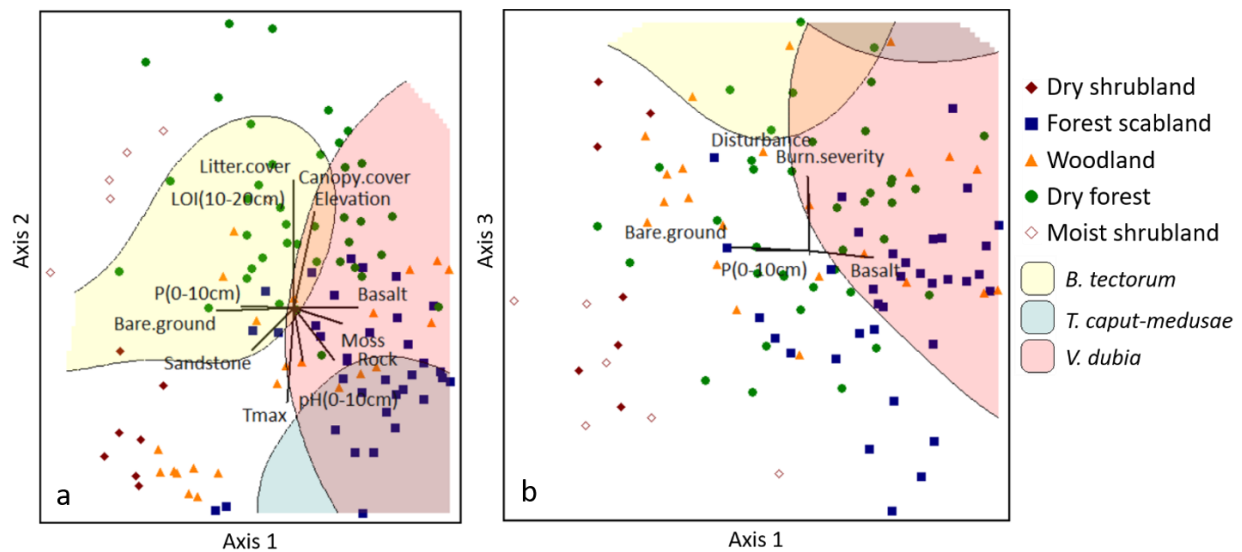
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## 2.8 Figures



**Figure 2.1** Location of sample plots within and just outside of seven fire perimeters (red polygons) in the Blue Mountains Ecoregion study area in northeastern Oregon, U.S.A.

In total, 110 plots (55 burned and 55 unburned) were sampled across seven fire perimeters within federally managed lands (light green areas).



**Figure 2.2** Ordination of sample plots in species space.

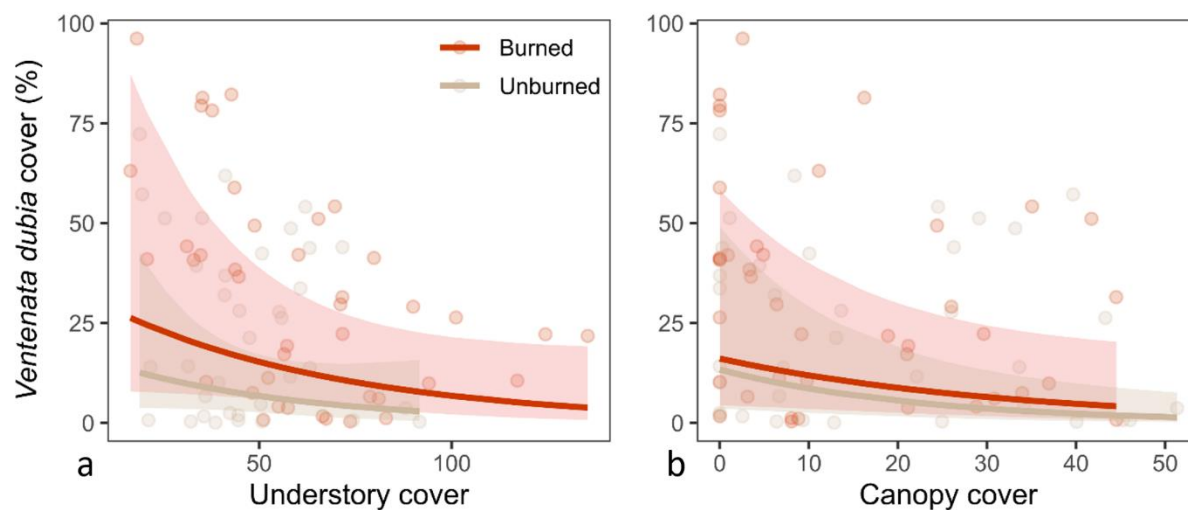
Species composition and environmental characteristics differed in sample plots with high *V. dubia* cover compared to sites with high cover of *B. tectorum* and *T. caput-medusae*. Nonparametric multidimensional scaling ordinations display sample plots in species space with Axis 1 rotated to load *V. dubia* cover. Sample plots are represented by their corresponding biophysical setting. Shaded polygons represent the top 20% of *V. dubia*, *B. tectorum*, and *T. caput-medusae* response surfaces in relation to the ordination axes ( $R^2 = 0.60, 0.24, 0.10$  respectively). Environmental variables linearly correlated with the ordination axes with  $R^2 > 0.2$  are displayed by vectors proportional to the direction and strength of the linear relationship. *V. dubia* and *B. tectorum* response surfaces separate along Axis 1 (**panel A**) and 3 (**panel B**). *V. dubia* and *T. caput-medusae* response surfaces separate along Axis 2 (**panel A**) and Axis 3 (**panel B**).





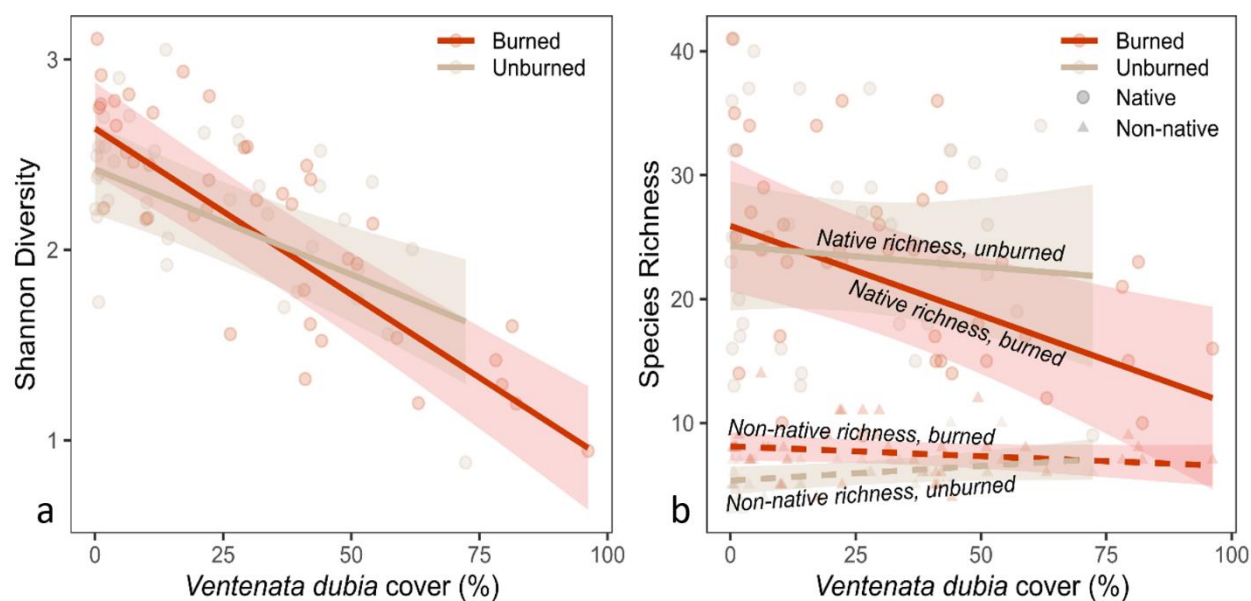
**Figure 2.3** *Ventenata dubia* invasion in forest scablands and surrounding forest.

*Ventenata dubia* heavily invaded burned and unburned historically sparsely vegetated and pyro-resistant “forest scablands” interspersed throughout the forested landscape. **Panel A** depicts an uninvaded, unburned forest scabland surrounded by mixed conifer forest. **Panel B** depicts a forest scabland heavily invaded with *V. dubia*. **Panel C** depicts a burned and invaded forest scabland.



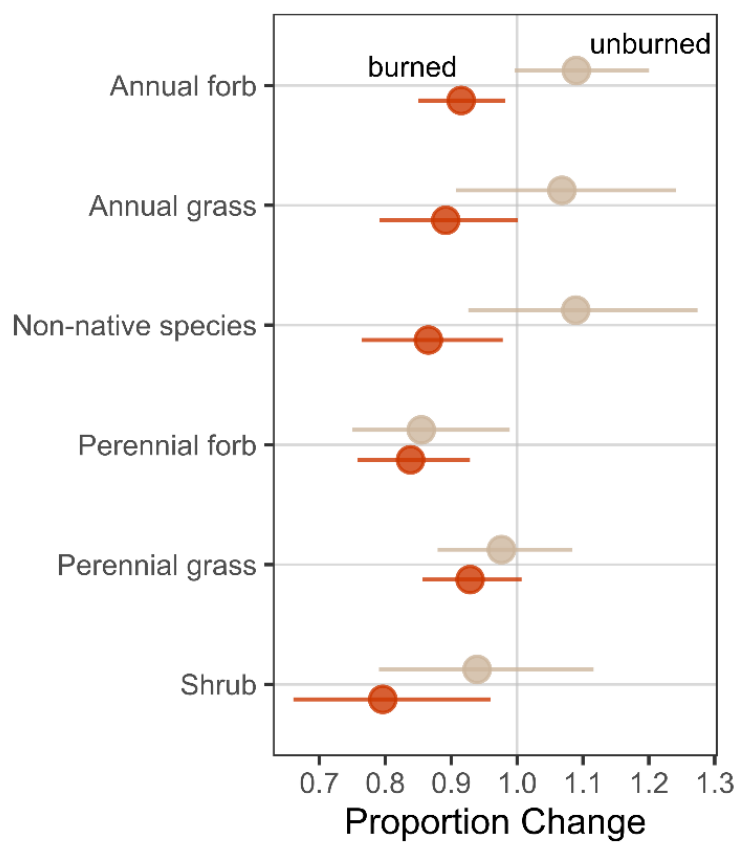
**Figure 2.4** *Ventenata dubia* response to understory foliar cover (excluding *V. dubia*; panel A) and canopy cover (panel B) in burned and unburned plots with 95% confidence intervals.

*Ventenata dubia* heavily invaded plots a wide range of understory and canopy cover, although the most heavily invaded plots (*V. dubia* cover > 75%) were burned with <50% understory cover and <20% canopy cover. Understory cover was recorded for each species at all strata allowing total understory cover to exceed 100%.

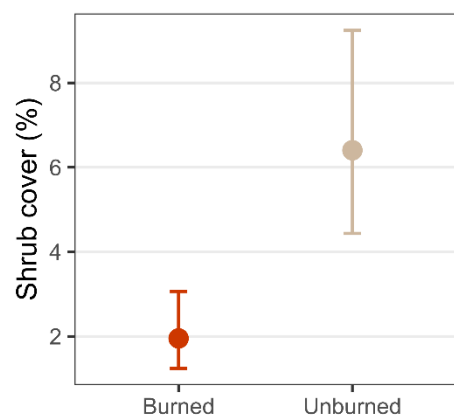


**Figure 2.5** Species richness and Shannon diversity response to *V. dubia* cover with 95% confidence intervals.

Shannon diversity decreased with increasing *V. dubia* cover in burned and unburned plots (estimates -0.02 and -0.01, 95% CIs -0.02 to -0.01 and -0.02 to -0.01 respectively). Native species richness decreased with increasing *V. dubia* cover in burned plots, but was not strongly related to *V. dubia* cover in unburned plots (estimates -0.14 and -0.03, 95% CIs -0.24 to -0.05 and -0.15 to 0.09 respectively), whereas non-native species richness was not strongly related to *V. dubia* cover in burned or unburned plots (estimates -0.01 and 0.03, 95% CIs -0.03 to 0.01 and 0.00 to 0.06 respectively).



**Figure 2.6** Estimates of the change in functional group cover for a 10% increase in *V. dubia* cover in burned and unburned plots with 95% confidence intervals. Values above 1.0 indicate an increase and below 1.0 indicate a decrease.



**Figure 2.7** Mean shrub cover in burned plots was less than one third of mean shrub cover in unburned plots (estimated ratio = 0.3; 95% CI 0.2 to 0.5) in plots where *V. dubia* was present (N = 77).

## 2.9 Tables

**Table 2.1 Biophysical settings across which vegetation sampling was conducted**

Biophysical Setting	Dominant Woody Species	Associated Species	Elevation* (m)	Soil Temp. Regime	No. of Plots
Dry shrubland	<i>Artemisia tridentata</i> subsp. <i>wyomingensis</i>	<i>Poa secunda</i> <i>Pseudoroegneria spicata</i>	750-1200	mesic	3 unburned; 4 burned
Forest scabland	<i>Artemisia rigida</i> / <i>Artemisia arbuscula</i>	<i>Poa secunda</i> <i>Danthonia unispicata</i>	850-1660	mesic-frigid	23 unburned; 12 burned
Woodland	<i>Juniperus occidentalis</i> / <i>Pinus ponderosa</i>	<i>Pseudoroegneria spicata</i> <i>Festuca idahoensis</i> <i>Poa secunda</i>	800-1550	mesic - frigid	8 unburned; 15 burned
Dry forest	<i>Pinus ponderosa</i> / <i>Pseudotsuga menziesii</i>	<i>Pseudoroegneria spicata</i> <i>Carex geyerii</i> <i>Festuca idahoensis</i>	1300-1600	mesic-frigid	16 unburned; 23 burned
Moist shrubland	<i>Artemisia tridentata</i> subsp. <i>vaseyana</i>	<i>Ericameria nauseosa</i> <i>Festuca idahoensis</i>	1800 - 2050	frigid - cryic	5 unburned; 1 burned

\*Elevation ranges represent the elevational range of sample plots within the study area



**Table 2.2 Ignition dates, acres burned, elevation range, and number of plots sampled within and within 1km of each fire perimeter**

<b>Fire Name</b>	<b>Ignition Date</b>	<b>Hectares burned</b>	<b>Elevation Range (m)</b>	<b>No. Plots sampled</b>
Fox	7/17/2014	3,780.2	1311 - 1601	26
South Fork Complex	7/31/2014	27,010.4	1257 - 2054	27
Corner Creek	6/29/2015	12,263.2	1334 - 1560	24
Cornet-Windy Ridge	8/10/2015	41,502.2	1146 - 1862	6
Canyon Creek Complex	8/12/2015	44,428.9	1462 - 1805	11
Emerson	7/25/2017	4,297.0	752 - 829	4
Whychus	8/10/2017	623.2	821 - 885	12

**Table 2.3 Indicator species for plots with greater than 15% *Ventenata dubia* cover**

<b>Species</b>	<b>IV</b>	<b>Mean</b>	<b>S.Dev</b>	<b>p-value</b>
<i>Bromus</i> spp. (annuals)	46.6	28.5	3.29	0.0002
<i>Agoseris heterophylla</i>	37.9	27.6	3.14	0.0062
<i>Draba verna</i>	37.3	30.5	2.63	0.0164
<i>Danthonia unispicata</i>	36.5	19.5	3.47	0.0002
<i>Blepharipappus scaber</i>	35.7	20.6	3.53	0.0008
<i>Holastium umbellatum</i>	34.0	20.9	3.33	0.0036



**Table 2.4 Shannon diversity and species richness response to *V. dubia* cover**

Interactions between *V. dubia* cover and plot level burn status for plots where *V. dubia* is present (N = 77). Burning most strongly influenced the effect of *V. dubia* cover on Shannon diversity and native species richness. Reported values are from an F-test with Kenward-Roger approximation.

<b>Response variable</b>	<b>F-statistic</b>	<b>Numerator df</b>	<b>Denominator df</b>	<b>p-value</b>
Shannon diversity	4.23	1	71.1	0.043
Native species richness	2.29	1	71.2	0.135
Non-native species richness	5.56	1	71.3	0.022

**Table 2.5 Functional group cover response to *V. dubia* cover:**

Interactions between *V. dubia* cover and burn status in plots where *V. dubia* is present (N = 77). Burning most strongly influenced the effect of *V. dubia* cover on annual forb, annual grass, and non-native species cover. a = Reported values are from an F-test with Kenward-Roger approximation. b = Shrub cover response to *V. dubia* was modeled with a Tweedie distribution to account for a high proportion of zeros and reported values are from an Analysis of Deviance with Wald chi-square tests.

Functional group response variable	F-statistic	Numerator df	Denominator df	p-value
Annual forb cover (%) <sup>a</sup>	8.83	1	71.1	0.004
Annual grass cover (%) <sup>a</sup>	3.46	1	70.6	0.067
Non-native species cover (%) <sup>a</sup>	5.10	1	71.3	0.027
Perennial forb cover (%) <sup>a</sup>	0.05	1	70.2	0.819
Perennial grass cover (%) <sup>a</sup>	0.53	1	71.9	0.471
	Chi-sq			Pr (>Chisq)
Shrub cover (%) <sup>b</sup>	1.62	1		0.20312

**CHAPTER 3**  
**COMMUNITY INVASION RESISTANCE IS INFLUENCED BY INTERACTIONS BETWEEN PLANT**  
**TRAITS AND SITE PRODUCTIVITY**

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## Abstract

Plant communities are predicted to be more resistant to invasion if they are highly productive, harbor species with similar functional traits to invaders, or support species with high competitive potential. However, the strength of competition may decrease with increasing abiotic stress if species more heavily invest in traits that confer stress tolerance over competitive ability, potentially influencing community trait-resistance relationships. Recent research examining how community traits influence invasion resistance has been predominantly focused on single vegetation types, and results between studies are often conflicting. Few studies have evaluated the extent to which abiotic factors and community traits interact to influence invasion along vegetation gradients. Here, we use an *in-situ* seed addition experiment to examine how above- and below-ground plant traits and vegetation type interact to influence community resistance to invasion by a recently introduced annual grass, *Ventenata dubia*, along a productivity gradient in eastern Oregon, U.S.A.

To measure invasion resistance, we evaluated *V. dubia* biomass in seeded subplots with varying trait compositions across three vegetation types situated along a productivity gradient: scab-flats (sparsely vegetated dwarf-shrublands), low sage-steppe, and ephemeral wet meadows. Trait-resistance relationships were highly context dependent. In wet meadows (the most productive sites), resistance to invasion increased with increasing resident biomass and as community weighted mean trait values for specific leaf area, fine-to-total root volume, and height become more similar to *V. dubia*'s trait values, although these relationships were relatively weak. We did not find evidence that neighboring species influenced invasion resistance in less productive vegetation types, in contrast to our expectations that facilitative interactions may increase with decreasing productivity as posited by the stress-gradient

hypothesis. Unlike *V. dubia* which heavily invaded all three vegetation types, introduced species with similar trait values, including *Bromus tectorum*, were not abundant throughout the study area demonstrating *V. dubia*'s unique ability to take advantage of available resources. Our results illustrate how community traits and site productivity interact to influence community resistance to invasion and highlight that communities with lower overall biomass and few functionally similar species to *V. dubia* may be at the greatest risk for invasion.

### 3.1 Introduction

Community resistance to invasion by introduced species is influenced by interactions with biotic and abiotic characteristics of the recipient community. These resistance factors are not mutually exclusive, and the strength and direction of biophysical interactions may vary across gradients in resource availability and environmental stress (Chesson 2000, VonHolle and Simberloff 2005). Studies of plant communities that investigate the local biotic factors influencing invasion, such as resident biomass and functional trait composition, often focus on a single biophysical setting or vegetation type and may neglect to consider how local biotic factors interact with abiotic site conditions and resource availability, such as available soil moisture (Byun et al. 2017). Understanding how above- and below-ground community traits and environment interact to influence invasion resistance is important for predicting potential impacts associated with introduced species, targeting management efforts, and developing generalizable invasion frameworks.

Multiple community assembly hypotheses have been developed to explain how community traits contribute to community assembly, biotic-interactions, and invasion resistance in plant ecology. Of these, three key hypotheses have emerged which we examine here. Community

productivity is posited to lead to higher competitive potential and invasion resistance as productive communities more completely utilize resources and leave fewer resources available for invaders (Gaudet & Keddy, 1988; Lulow, 2006). We refer to this hypothesis hereafter as the “productivity-resistance hypothesis”. However, community functional trait composition may be a stronger predictor of invasion resistance than biomass alone if some traits increase community competitive potential more than others. The limiting similarity hypothesis posits that ecologically similar species with similar trait values have greater niche overlap and compete more strongly for limited resources than dissimilar species (MacArthur and Levins 1967, Kunstler et al. 2012), hereafter the “trait similarity hypothesis”. Alternatively, the competition-trait hierarchy hypothesis predicts that competitive ability is directionally ranked, with differences in traits related to competition reflecting disparities in fitness and competitive ability (Kunstler et al. 2012), hereafter the “trait hierarchy hypothesis”.

Under the trait similarity hypothesis, communities composed of species with similar trait values to invaders are expected to compete more strongly for resources in shared niches, resulting in greater invasion resistance than communities with dissimilar traits. Functional similarity between resident species and potential invaders has been found to increase community resistance to invasion in some cases; however, findings between studies are often inconsistent (Price and Pärtel 2013). Invasion resistance through trait similarity can be maintained by different mechanisms with distinct ecological assumptions which can be measured different ways, potentially contributing to conflicting findings (Gallien et al. 2014). Competition with invaders may be driven by several species and influenced by each species’ relative abundance, or may be driven by only those species that are most similar to the invader, irrespective of their abundance (Thuiller et al. 2010). However, all indices of trait similarity may be poor predictors

of invasion resistance if there is an insufficient degree of niche overlap present, or if invasion is more strongly influenced by other processes such as fitness differences (Hess et al. 2020).

Trait hierarchies may influence invasion resistance when trait variations between resident and introduced species reflect competition and fitness differences rather than niche overlap. Many recent studies have found such hierarchies to be stronger drivers of community resistance to invasion than trait similarity (Lai et al. 2015, Sheppard 2019). For example, species with traits that confer high competitive potential for limited surface soil resources, such as high specific root length, low root-to-shoot biomass, and low leaf nitrogen concentration, suppressed invader growth more strongly than species with similar trait values to an invader in a Californian serpentine grassland (Funk and Wolf 2016).

Despite the expanding body of literature exploring relationships between community traits and invasion resistance, inconsistencies across studies has slowed the development of generalizable community trait-resistance frameworks (Price and Pärtel 2013, Garbowski et al. 2020, Hess et al. 2020). Such inconsistencies may be in part attributed to context dependencies driven by interactions between community trait-invasion relationships and abiotic conditions.

Environmental stress has been shown to alter the strength and direction of species interactions and plant community-invasion resistance relationships. Competitive interactions are predicted to be weaker in less productive communities (Grime 1979), and may shift from competitive to facilitative in stressful environments when neighboring species ameliorate physical environmental conditions as predicted by the “stress-gradient hypothesis” (Bertness and Callaway 1994, Hacker and Gaines 1997). That is, resident biomass, community-trait similarity, and trait-hierarchies may contribute more strongly to community invasion-resistance in low stress, resource rich environments than in stressful environments with limited resources. The

presence of resident species may even facilitate invasion in high stress environments if the characteristics of the community or species helps to ameliorate abiotic stressors (Von Holle 2013, Zarnetske et al. 2013, Lucero et al. 2019). Additionally, the relative importance of community traits in conferring invasion resistance and the strength of trait-resistance relationships may differ depending on environmental conditions and resource availability (Conti et al. 2018, Funk 2021). Traits related to high rates of resource acquisition such as high height and specific leaf area may contribute strongly to community resistance in low stress and resource rich environments, while traits associated with stress tolerance and conservative resource use, such as low specific leaf area and low leaf nitrogen may be more important in high stress and resource limited communities (Funk and Wolf 2016).

The relatively recent invasion of a Eurasian annual grass, *Ventenata dubia*, in North America's Inland Pacific Northwest provides an important and relevant opportunity to disentangle the three invasion hypotheses. The rapid expansion of *V. dubia* into previously uninvaded natural areas (Tortorelli et al. 2020) and its potential to alter ecosystem processes through changing fuel characteristics and fire behavior have contributed to this species' high management concern (Kerns et al. 2020). Despite its high-risk profile, relatively little is known regarding the factors influencing community susceptibility or resistance to *V. dubia* invasion, or how community-resistance relationships vary across vegetation types. Understanding how community traits and site conditions interact to influence resistance to this aggressive invader can aid the development of targeted management approaches while helping to build generalizable resistance frameworks.

Here, we use an *in-situ* field experiment to test how three community assembly hypotheses predict resistance to *V. dubia* invasion, and how trait-resistance relationships vary with biotic and



abiotic context. We examine how (1) resident biomass, (2) trait similarity, and (3) trait hierarchy, influence invasion resistance in three distinct vegetation types situated along a vegetative productivity gradient (Fig. 3.1).

## 3.2 Materials and Methods

### 3.2.1 Study area

The study was conducted over summer 2019 through 2020 in the Ochoco National Forest of eastern Oregon's Blue Mountains, U.S.A. The mixed conifer forest ecosystems of the Blue Mountains are situated on an expansive lava plateau positioned just east of the Cascade Mountains. The forests are intermixed with large patches of shallow, basaltic soils supporting ephemeral wet meadows and xeric shrublands. This area receives between 19 and 52 cm of precipitation per year, with the majority falling between November and June (Western Regional Climate Center 2021). Precipitation during the sampling season was slightly higher than average, with more rain falling in the late summer and early fall (Appendix S1).

### 3.2.2 Vegetation gradient

Study sites included three non-forest vegetation types embedded within the larger forested landscape that are frequently invaded by *V. dubia*: ephemeral wet meadows, low sage-steppe, and scab-flats (Fig. 3.2). The vegetation types have distinct floral compositions that vary along a productivity gradient likely driven by differences in soil depth and available soil moisture (Table 3.1). Ephemeral wet meadows are the most productive and have the deepest soils of the three vegetation types (Paulson 1977). These sites are characterized by a perched water table and saturated soils in spring and early summer, allowing them to support wetland obligate species including *Juncus* spp. and *Camas quamash* (Johnson and Swanson 2005). Of the two shrubland

vegetation types, scab-flats are the least productive with foliar cover typically under 20% and very shallow soils (Paulson 1977, Johnson and Swanson 2005). These rocky sites support low cover of *Artemisia rigida*, the shallow-rooted bunchgrass *Poa secunda*, and various annual and perennial forbs. Low sage-steppe falls between the wet meadows and scab-flats along the productivity gradient. This vegetation type has moderate foliar cover and deeper, better draining soils than scab-flats that support characteristic *Artemisia arbuscula* and deep-rooted perennial bunchgrasses, including *Pseudoroegneria spicata*, along with various annual and perennial forbs (Paulson 1977). The three vegetation types often exist in close proximity to one another and are exposed to harsh growing conditions and similar climatic extremes.

We chose the three vegetation types to represent a vegetative productivity gradient based on plant associations and soil descriptions from the Ochoco National Forest Soil Resource Inventory (Paulson 1977) and consultation with local soil and vegetation experts. We examined the extent to which the sampled vegetation types represented a true productivity gradient, and found that mean biomass differed between the three vegetation types with wet meadows being the most productive, followed by low sage-steppe, and scab-flats (Table 3.1; Appendix B.2).

### *Experimental Design and Implementation*

We conducted an *in-situ* experiment to measure community resistance to invasion by *V. dubia* across the three vegetation types, using a seed addition experiment to control propagule pressure and invasion intensity. Over June through August 2019, we installed 5 experimental blocks across the study region consisting of one plot in each of the three vegetation types. Distance between blocks ranged from 4.2 km to 17.4 km. Each plot contained 7 randomly selected subplots (20 x 20 cm) that varied naturally in species and functional trait composition. Subplots were arranged in a grid positioned so that all subplots fell within the target vegetation type. In

total, we installed 105 subplots (5 blocks x 3 vegetation types/plots x 7 subplots). Distances between neighboring subplots ranged from 1 m to 3 m.

We chose to conduct the experiment at a neighborhood scale (20 cm x 20 cm) to focus the study on interactions between *V. dubia* and its immediate neighboring species. Given *V. dubia*'s slight structure and minute root system, we assume the interactions are strongest at relatively small spatial scales. However, the restricted subplot size resulted in lower species richness and trait diversity present in local communities, and may not accurately represent trait compositions in larger communities. Species richness in subplots ranged from 4-17 species (Table 3.1). We limited the study to investigate interactions between *V. dubia* and herbaceous forbs and grasses because shrubs were not present in all plots and to avoid removing ecologically important *Artemisia* spp. when collecting biomass for testing the productivity-resistance hypothesis. Accordingly, subplots were located at least 50 cm from the edge of the nearest dwarf shrub canopy. At the plot level, dwarf shrub cover ranged from 5-15% in low sage-steppe and scab-flats. Sample plots were installed in currently invaded areas to ensure that *V. dubia* was adapted to the environmental conditions of each plot and to avoid spreading *V. dubia* into uninvaded areas. In subplots where *V. dubia* was already established, community composition and biomass may have been influenced by the invader. In a previous observational field study, we found that *V. dubia* cover increased with decreasing Shannon Diversity (Tortorelli et al. 2020). However, whether diversity was reduced by invasion or diversity conferred invasion resistance was unknown.

Subplots were prepared by removing any existing *V. dubia* then adding a measured aliquot of seed to minimize the effects of natural variability in *V. dubia* propagules at each subplot. Existing *V. dubia* was hand pulled from inside subplots and from a 25 cm buffer surrounding

each subplot to reduce natural recruitment of *V. dubia*. Disturbance from hand pulling was minimal. The seed was collected from just outside each plot in early August, combined, hand cleaned, weighed into equal portions, and tested for viability with a tetrazolium chloride test at the Oregon State University seed lab. Seeds were 91% viable. We broadcast seeds into subplots at a rate of approximately 500 seeds (0.41 g) per subplot (12,500 seeds/m<sup>2</sup>) in late August 2019, because *V. dubia* is a cool season, C3 annual, known to germinate in the fall (Wallace et al. 2015). Seed amounts were chosen to represent a realistic high level of invasion assuming that individuals generally produce 15 to 35 seeds per plant (Wallace et al. 2015) and we observed hundreds of individual plants in our heavily invaded subplots prior to seeding. We seeded at a high invasion level to increase potential biotic interactions within the subplots and to dampen the effect of the residual seed bank between subplots. We expected the effect of residual seed bank to be relatively low given the short seed bank lifespan of *V. dubia* (less than 3 years; Wallace et al. 2015). However, to measure natural *V. dubia* recruitment, we installed an additional 3 subplots at each plot (n = 45) as “unseeded controls” in which we removed *V. dubia* from all subplots but did not add *V. dubia* seed (Fig. B.3.1). We installed 10 cm high cages around each subplot composed of steel wire hardware cloth with 3mm openings at the time of seeding to limit seeds from blowing out or into subplots.

We revisited all subplots in late June 2020 to measure percent foliar cover of plant species and harvest all above-ground biomass in each subplot. *Ventenata dubia* biomass and non-*V. dubia* (resident) biomass were separated, dried at 55° C for 42 hours, and weighed to the nearest 0.01 g. This study was conducted over a single growing season and care should be taken when generalizing results to years with climatic conditions that differ from those that occurred over the sapling period. Higher fall precipitation observed over the sample period (Appendix S1) may

have increased the germination success of fall-germinating annual grasses (including *V. dubia*) relative to spring-germinating native annual forbs compared to an average year.

### *Species functional traits*

We sampled and calculated above and belowground functional traits from 37 of the most abundant species present in the subplots (Table B.4.1). To reduce the total number of species included in the analysis down to 37, we excluded species if their foliar cover was consistently less than 0.5% or they occurred in fewer than three subplots (2% of subplots). To quantify the trait potential of each species in conditions where competitive strategies are most clearly expressed, we collected samples between May and July 2020 from reproductive individuals, either in flower or in seed, from the least stressful environment possible. Most species were collected from wet meadows ( $n = 31$ ; Table B.4.2). However, many species, including *V. dubia*, displayed trait plasticity across the vegetation types with individuals appearing generally more robust in wet meadows than low sage-steppe or scab-flat plots. Thus, our trait metrics may overestimate trait values in less productive sites for traits that are more strongly expressed in more productive sites.

We focused on seven functional traits related to competitive ability, potential growth rate, carbon capture, nitrogen acquisition, resource allocation, and root longevity (Table 3.1) following protocols presented in Cornelissen et al. (2003). For above-ground traits, two young, fully expanded leaves per individual were harvested, scanned for leaf area using Easy Leaf Area software (Easlon and Bloom 2014), dried, weighed to calculate specific leaf area, and analyzed for percent leaf nitrogen concentration (Central Analytical Laboratory, Corvallis, OR, USA).

For below-ground and whole plant traits, 4-7 individuals per species were harvested by digging up the entire root system, when possible (Table B.4.2). Roots were washed, dried, and

scanned using WinRHIZO image analysis system to determine total root length, root diameter, and fine-to-total root volume ratio (<2mm; Regent Instruments Inc., 2019). Above and belowground biomass was separated for each species, dried at 55°C for 48 hours, and weighed to calculate root:shoot. Species trait values were averaged across individuals and log transformed. Log-transformed trait values were mean centered and scaled by standard deviation to obtain standardized trait values for each species for comparisons (hereafter “trait values”). Community weighted mean (CWM) trait values were calculated for each subplot as the mean trait value weighted by proportional foliar cover of each species present.

### 3.2.3 Calculating community metrics

We used the following “community metrics” to calculate community resident biomass and trait values for each of the proposed assembly hypotheses, following Gallien et al. (2014) and Catford et al. (2019). To characterize the community in relation to the first hypothesis, productivity-resistance, we calculated the **resident biomass** metric as the sum of all above-ground biomass (excluding *V. dubia*) in each subplot as an indication of community productivity.

We applied two different metrics to characterize the second hypothesis, trait similarity, to account for differences in the relative importance of the entire community versus only the most similar species in conferring invasion resistance (Gallien et al. 2014; Thuiller et al. 2010). The **weighted mean dissimilarity** metric, also known as absolute trait distance, was calculated as the absolute value of the difference between the CWM trait values (excluding *V. dubia*) and *V. dubia*’s trait values for each of our seven functional traits at each subplot;  $(|\overline{CWM} - V. dubia|)$ . This metric indicates the degree of dissimilarity and potential niche overlap between *V. dubia* and the established community for each trait (Lai et al. 2015). Communities with high weighted mean dissimilarity likely have less niche overlap with *V. dubia* than communities with low

weighted mean dissimilarity. To indicate potential niche overlap between *V. dubia* and the functionally closest neighbors (Gallien et al. 2014), we calculated the ***nearest species dissimilarity*** metric as the difference between the trait value of the species that have trait values directly above ( $\bar{a}$ ) and below ( $\bar{b}$ ) those of *V. dubia* for each functional trait and at each subplot; ( $\bar{a} < V.dubia < \bar{b}$ ; *nearest species dissimilarity* =  $\bar{b} - \bar{a}$ ). Additional information on calculating nearest species dissimilarity is presented in Appendix B.3.

To characterize the third hypothesis, trait hierarchy, we calculated the ***hierarchical distance*** metric as the difference between the CWM trait values and *V. dubia*'s trait values for each functional trait at each subplot; ( $\overline{CWM} - V.dubia$ ). Negative values indicate that the CWM was lower than *V. dubia*'s trait value and positive values indicate that the CWM was higher than *V. dubia*'s trait value. The metric indicates directional fitness differences between communities and *V. dubia* according to the trait-hierarchy hypothesis (Lai et al. 2015, Catford et al. 2019).

### 3.3 Statistical Analysis

#### 3.3.1 Examining species and community traits

We examined trait similarity between resident species and *V. dubia* using non-metric multidimensional scaling (NMS) ordinations with species in trait space. To examine how the community trait distribution and trait potential (from the most productive vegetation type) differed between vegetation types, we plotted subplots in CWM trait space by vegetation type. NMS ordinations were performed using the Bray-Curtis distance measure with two-dimensions and random starting locations (Bray and Curtis 1957). Species and community trait values were log transformed (to account for them being log-normally distributed), standardized, and shifted by the minimum value of each trait so that all values were positive because Bray-Curtis

dissimilarities cannot be calculated for negative values. To further examine the extent to which CWM trait similarity to *V. dubia* varied by vegetation type, we calculated Euclidean distance between CWM and *V. dubia* trait values for each subplot and compared distances between vegetation types (Table B.5.1; Fig. B.5.1-B.5.2).

### ***3.3.2 Community traits x vegetation gradient effect on invasion resistance***

We tested the effect of our community metrics (resident biomass, weighted mean dissimilarity, nearest species dissimilarity, and hierarchical distance) on invasion resistance using linear mixed effects models. Each model examined the response of *V. dubia* biomass to a single community trait (e.g. height-hierarchical distance) and interaction with vegetation type as a factor. Biomass measurements were log transformed to meet the assumptions of linear modeling. Random intercepts were included for plots nested within experimental blocks. We explored different options for modeling community trait values including reducing trait dimensionality using multivariate distance metrics (Table B.5.1). However, we chose to base our analysis on individual trait models to avoid issues with collinearity among traits (Fig. B.5.3), to retain high interpretability (e.g. compared to reducing dimensionality using a multi-trait community metric, multivariate distance estimates, or ordination axes), and to maintain appropriate model sizes considering our blocked sampling design and inclusion of an interaction. To identify which assembly hypotheses best explained invasion resistance, we compared goodness-of-fit between individual models using pseudo marginal R-squared (hereafter “marginal  $r^2$ ”; Nakagawa & Schielzeth 2013).

Statistical analyses were performed in R version 4.0.3 using the package lme4 (Bates et al. 2015) for model fitting and performance (Lüdecke et al. 2021). The package r2glmm (Jaeger 2017) was used for computing marginal  $r^2$  following Nakagawa and Schielzeth (2013) and AICc



values were calculated from MuMIn (Barton 2020). Emmeans was used for slope comparisons (Russell 2021). We used the package car for testing interaction effects using type II Wald chi-square tests (Fox and Weisberg 2019) and vegan for NMS ordinations (Oksanen et al. 2019).

### 3.4 Results

#### 3.4.1 Comparison of species functional and community traits

Overall *V. dubia*'s trait values were most similar to neighboring annual and shallow-rooted perennial graminoids, including two introduced annual grasses, *Bromus tectorum* and *Bromus arvensis* (Fig. 3.3). These introduced grasses were not abundant throughout the study area, with a combined average cover of less than 4% (Fig. 3.3). On average, *V. dubia* had slightly shorter roots and lower root diameter compared to other introduced annual grasses and lower root:shoot, root diameter, and leaf N and higher fine-to-total root volume and SLA compared to most native residents (Fig. 3.3; Table B.4.2). The most abundant resident species throughout our subplots was *P. secunda* with average cover of 7.5%.

CWM trait values were highly variable amongst subplots and within vegetation types (Fig. B.5.4). There was considerable overlap in CWM trait values between vegetation types. However, on average, wet meadows had higher root diameter and shorter total root length, low sage-steppe had slightly higher fine-to-total root volume and height, and scab-flats had higher root:shoot and lower SLA than other vegetation types (Fig. B.5.4). Stress for the species and subplot two-dimensional NMS solutions were 0.13 and 0.11 respectively. Euclidean distances calculated between *V. dubia* and CWM trait values were highly variable between subplots (Fig. B.5.2). While mean Euclidean distance did not strongly differ between vegetation types, subplots in scab-flats generally had slightly higher Euclidean distances than those in low sage-steppe or wet

meadows and the lowest Euclidean distances were recorded from subplots in low sage-steppe (Fig. B.5.2).

The range of CWM trait values across all subplots generally fell entirely above or below *V. dubia*'s trait values depending on the trait, rather than some subplots having higher values and some lower, indicated by the presence of only negative or positive hierarchical distance values represented for a single trait (Fig. 3.4c). *Ventenata dubia* generally had higher height, SLA, and fine-to-total root volume and lower leaf N, root:shoot, root diameter, and root length than CWM trait values.

### 3.4.2 Community metrics $\times$ vegetation gradient effect on invasion resistance

*Ventenata dubia* biomass response to community metrics were variable and highly context dependent. When considering all vegetation types, community metrics were generally weak predictors of *V. dubia* biomass (marginal  $r^2$  for all models  $< 0.1$ ; Table B.6.1). The strongest predictors of *V. dubia* biomass were SLA-weighted mean dissimilarity, SLA-hierarchical distance, and resident biomass (marginal  $r^2 = 0.081, 0.081, \text{ and } 0.077$ , respectively; Fig. 3.4). We found no evidence of an effect of nearest species dissimilarity on *V. dubia* biomass for any trait.

The strength and direction of community metric-*V. dubia* relationships often depended on vegetation type. Community metric-*V. dubia* relationships were stronger in wet meadows than scab-flats or low sage-steppe for resident biomass and for all traits except root:shoot and root length for weighted mean dissimilarity and hierarchical distance metrics. While the strength of many trait-vegetation type interactions was uncertain given high variance in the data, we found evidence that vegetation type interacted with SLA-hierarchical distance (chi-squared = 4.95 [ $p = 0.08$ ]), SLA-weighted mean dissimilarity and (4.90 [ $p = 0.09$ ]), and resident biomass (4.06 [ $p = 0.13$ ]) to influence *V. dubia* biomass (Table B.6.2). In wet meadows, *V. dubia* decreased with

increasing resident biomass (estimate: -0.56 [95% CI: -0.95, -0.17]) and as CWM fine-to-total root volume, height, and SLA became more similar to *V. dubia* (Fig. 3.4; Table B.6.3).

*Ventenata dubia* also decreased as CWM leaf N and root diameter approached *V. dubia*'s trait value in wet meadows, but these results are uncertain given high variances around the mean. In less productive low sage-steppe and scab-flats, we did not find evidence to suggest that resident biomass or community traits strongly influenced *V. dubia* biomass (Fig. 3.4; Table B.6.3).

### 3.5 Discussion

Community trait-resistance relationships varied by community metric, trait, and vegetation type, with the strongest relationships almost always occurring in the most productive vegetation type, wet meadows. Our findings suggest that community resistance mechanisms and species interactions are highly context dependent, and are likely to be strongest in productive sites in concordance with the productivity-resistance and stress gradient hypotheses. However, *V. dubia* successfully invaded and became abundant in communities regardless of vegetation type, community trait composition, or resident biomass, indicating that it may experience relatively little competition and niche overlap with herbaceous neighbors, and the invasibility of communities may be more strongly influenced by unmeasured microsite factors. Despite sharing similar functional traits to *V. dubia*, other annual grasses were not abundant throughout our sample sites, highlighting the novelty of the *V. dubia* invasion. Our findings indicate that *V. dubia*'s success may be driven by additional physiological or other mechanisms distinct from the above- and below-ground traits that we included in our analysis.

Resident biomass was one of the strongest drivers of community resistance to *V. dubia*, consistent with the productivity-resistance hypothesis. However, resident biomass only conferred

community resistance in wet meadows where site productivity was relatively high. Our findings resonate with past studies that reported stronger effects of biomass on invasion resistance to an introduced perennial forb than individual species' traits (including height, root:shoot, and leaf area) in productive wetland communities (Gaudett & Kelly 1988) and higher community resistance to annual grass invasion in areas with abundant perennial bunchgrasses (Lulow 2006). Such resistance may be attributed to decreased general resource availability including light, water, soil nutrients, and physical spaces for the invader to establish as community abundance increases (Chambers et al. 2007).

Invasion was lowest when CWM trait values were similar to *V. dubia*'s trait value in the most productive vegetation type, wet meadows, indicating that functionally similar communities may be more resistant to *V. dubia* through greater niche overlap when they also have high biomass, consistent with the trait similarity hypothesis. However, separating the relative importance of trait similarity and trait hierarchy resistance mechanisms is difficult because *V. dubia*'s trait values fell above or below the CWM trait values for each trait in almost every community. For example, it is unclear whether the strong relationships observed between *V. dubia* and SLA in wet meadows was driven by a fitness advantage of species with high SLA or niche differentiation (as species with higher SLA were also more similar to *V. dubia*). The same can be said for relationships with height and fine-to-total root volume. Additionally, the extent to which different traits confer invasion resistance remains unclear. For example, while high SLA and leaf N are commonly associated with competitive potential and resource use, especially in resource rich environments (Cornelissen et al. 2003), some studies have found that species with

low SLA and leaf N increase biotic resistance to invaders, including those with higher SLA, particularly in environments with limited resources (Funk and Wolf 2016, Conti et al. 2018).

In our case, distinguishing between trait similarity and trait hierarchy resistance mechanisms may not be especially relevant for identifying areas at high risk for invasion because *V. dubia*'s trait values nearly always fell outside the range of naturally occurring CWM trait values in these commonly invaded vegetation types. However, for restoration treatments where there is the opportunity to introduce different species to the community, it is important to understand if communities with greater competitive potential (measured through hierarchical distance) compete more strongly with *V. dubia*. Further investigation is needed in vegetation types with a range of CWM trait values that fall above and below *V. dubia*'s trait values (e.g. invaded oak savannahs or Palouse prairies) to address whether trait hierarchies or similarity contribute more strongly to invasion resistance.

Although we were unable to differentiate the effect of trait hierarchies from trait similarities, our findings suggest that community resistance is influenced by multiple or the most abundant species rather than one or two of the most similar species, since weighted mean dissimilarity was clearly a stronger predictor of community resistance than nearest species dissimilarity. Our results resonate with those of Gallien et al. (2014) who reported that community metrics involving the entire community were more successful at measuring competition effects than metrics involving only the most similar species.

The effects of resident biomass, weighted mean dissimilarity, and hierarchical distance on community resistance were almost always strongest in the most productive vegetation type. If effect sizes accurately represent the strength of community-resistance interactions (despite high variability in the data contributing to uncertainty), our results would be consistent with the stress

gradient hypothesis which posits that competitive interactions decrease in strength as environmental stress increases (Bertness and Callaway, 1994, Hacker and Gains, 1997). The weak trait-resistance relationships present in scab-flats and low sage-steppe may be explained by the overall low cover and biomass, allowing *V. dubia* to take advantage of the abundance of physical space for establishment and resources that may be less available to resident species. Species with similar traits may contribute more to invasion resistance in productive sites where there is greater niche overlap, fewer unused resources, and less physical space available for establishment. We suggest that mixed results observed in many studies evaluating the effect of community trait similarity on community resistance (see Price & Pärtel, 2013) may in part be driven by differences in overall site productivity leading to differences in the competitive potential of resident species.

In contrast to experimental findings from perennial grass invasion along a coastal environmental stress gradient (Zarnetske et al. 2013), we did not find evidence that resident herbaceous biomass facilitated invasion in semi-arid vegetation types with high environmental stress. If this were the case, *V. dubia* would have increased with increasing resident biomass in the least productive scab-flat sites. This may demonstrate that either herbaceous species in these vegetation types are weak facilitators and do little to ameliorate stressful conditions for their neighbors, or that *V. dubia* is not strongly influenced by this particular stress gradient and does not require amelioration to thrive in these environments.

We did not consider the effect of dwarf shrubs in this study as they were generally sparse in our communities and were not present in all vegetation types. However, where they are present in scab-flats and low sage-steppe they likely play important ecological roles by creating patches of nutrient enrichment beneath their canopies (Bechtold and Inouye 2007). Recent studies have

found facilitative effects of shrubs species on abundance of introduced annuals in otherwise stressful environments (Lucero et al. 2019). Further research is required to understand the effects of shrubs on *V. dubia* establishment and growth.

*Ventenata dubia* had similar trait values to some resident species, including two introduced invasive annual grasses *B. tectorum* and *B. arvensis*, however these functionally similar graminoids were not abundant across the vegetation gradient, despite maintaining a scattered presence throughout the area for decades and heavily invading nearby *Artemisia tridentata* (big sagebrush) and burned forest communities (Johnson and Swanson 2005). This finding reflects the novelty of *V. dubia*'s invasion into shallow soil communities in which few functionally similar native or introduced species have become abundant (Tortorelli et al. 2020). Furthermore, trait similarities to resident species suggest that standard below- and above-ground traits such as those we present here may not be driving *V. dubia*'s relative success in these areas. Instead, success may be attributed to physiological differences such as cold tolerance, phenology, fecundity, or enemy release (Levine et al. 2004).

This study highlights the importance of testing hypotheses in various contexts by demonstrating that community metrics and site productivity interact to influence invasion resistance. Our findings support community assembly hypotheses by showing that resident biomass and communities with similar SLA, fine-to-total root volume, and height as *V. dubia* conferred some invasion resistance, but only in the most productive vegetation type, and these relationships were rather weak. *Ventenata dubia* successfully invaded communities regardless of resident biomass and community traits demonstrating high invasion potential, particularly in ecosystems that were previously thought to be resistant to annual grass invasion. These findings highlight the novelty of the *V. dubia* invasion, identify communities that are at high risk of

invasion (less productive vegetation types and wet meadows with low biomass and few functionally similar species), and contribute to the development of generalizable resistance frameworks that may apply to new invaders and environments.

### **3.6 Acknowledgments and Data**

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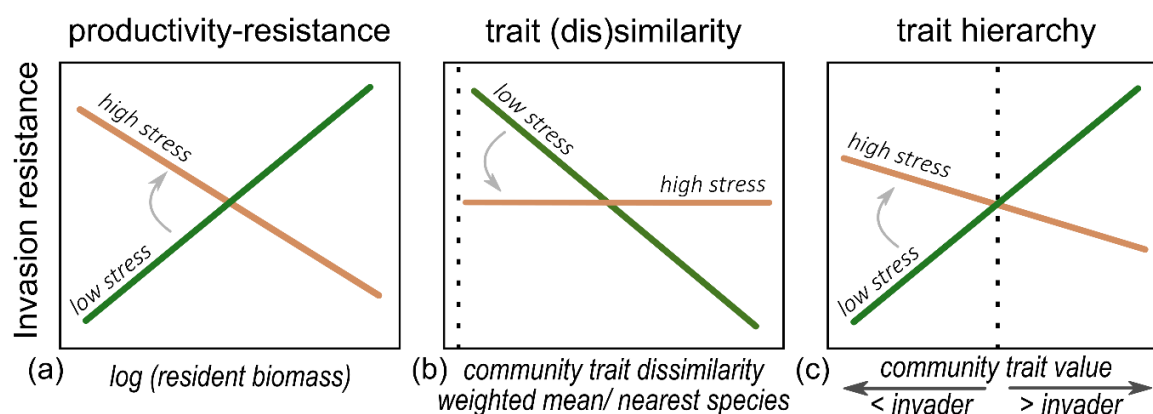
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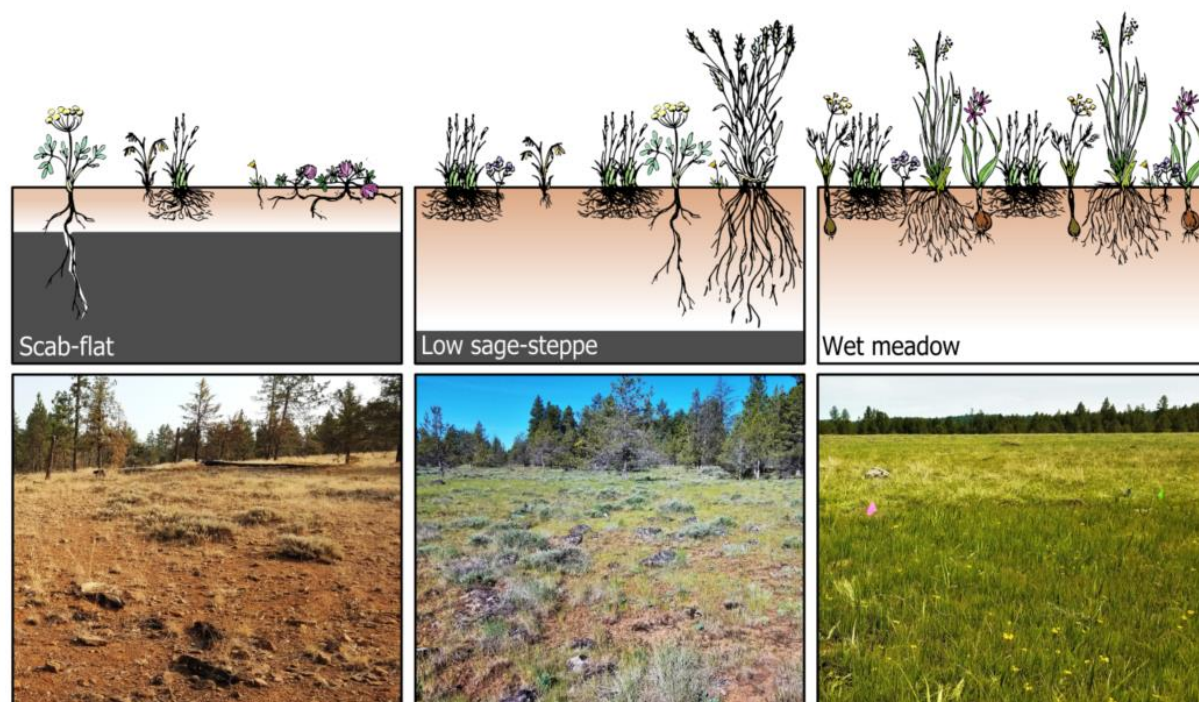
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### 3.8 Figures

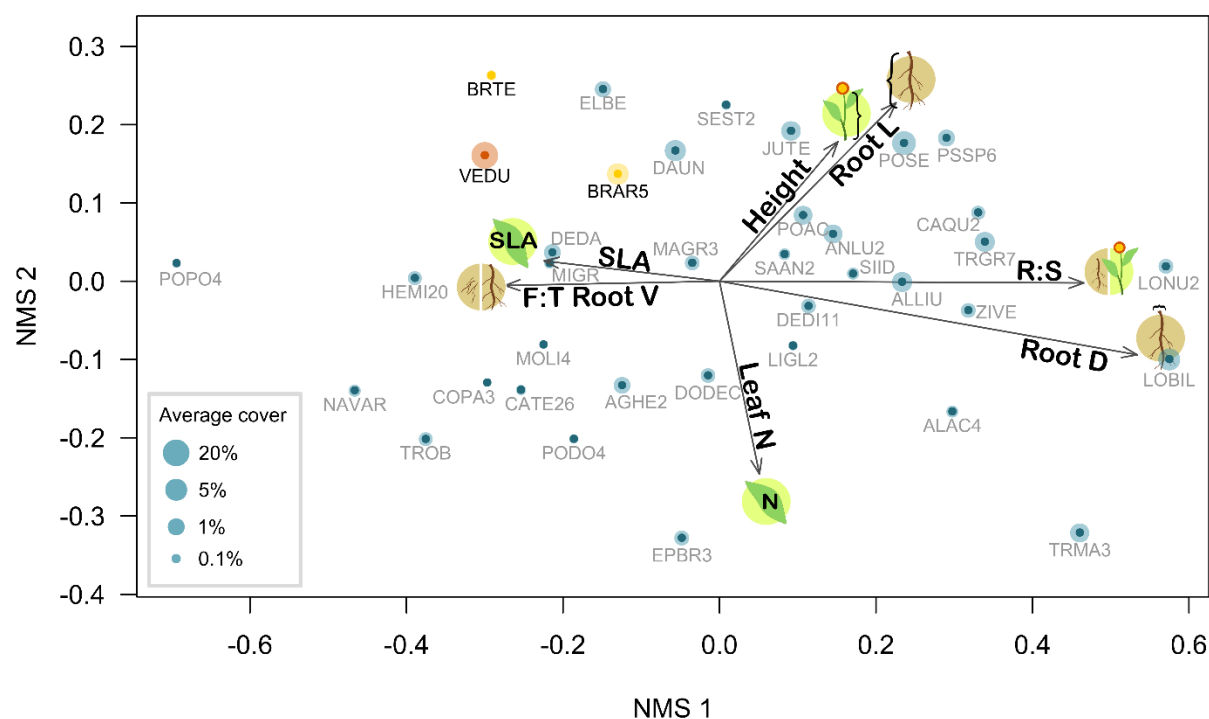


**Figure 3.1** Three community assembly hypotheses and potential interactions with environmental stress.

(a) Productivity-resistance relationships are predicted to be positive in low stress environments where competition between resident species and invaders is strongest. However, productivity-resistance relationships may become negative in high stress environments if residents ameliorate stressful abiotic conditions and facilitate invasion. (b) Invasion resistance is expected to decrease with increasing trait dissimilarity in low stress environments where competition for resources is predicted to be strongest, but these relationships may be less pronounced as abiotic stress increases and competition between species weakens. (c) The trait hierarchy hypothesis posits that invasion resistance will either increase or decrease as community trait values exceed those of the invader, depending on the trait. The direction of trait-resistance relationship may be influenced by environmental conditions.

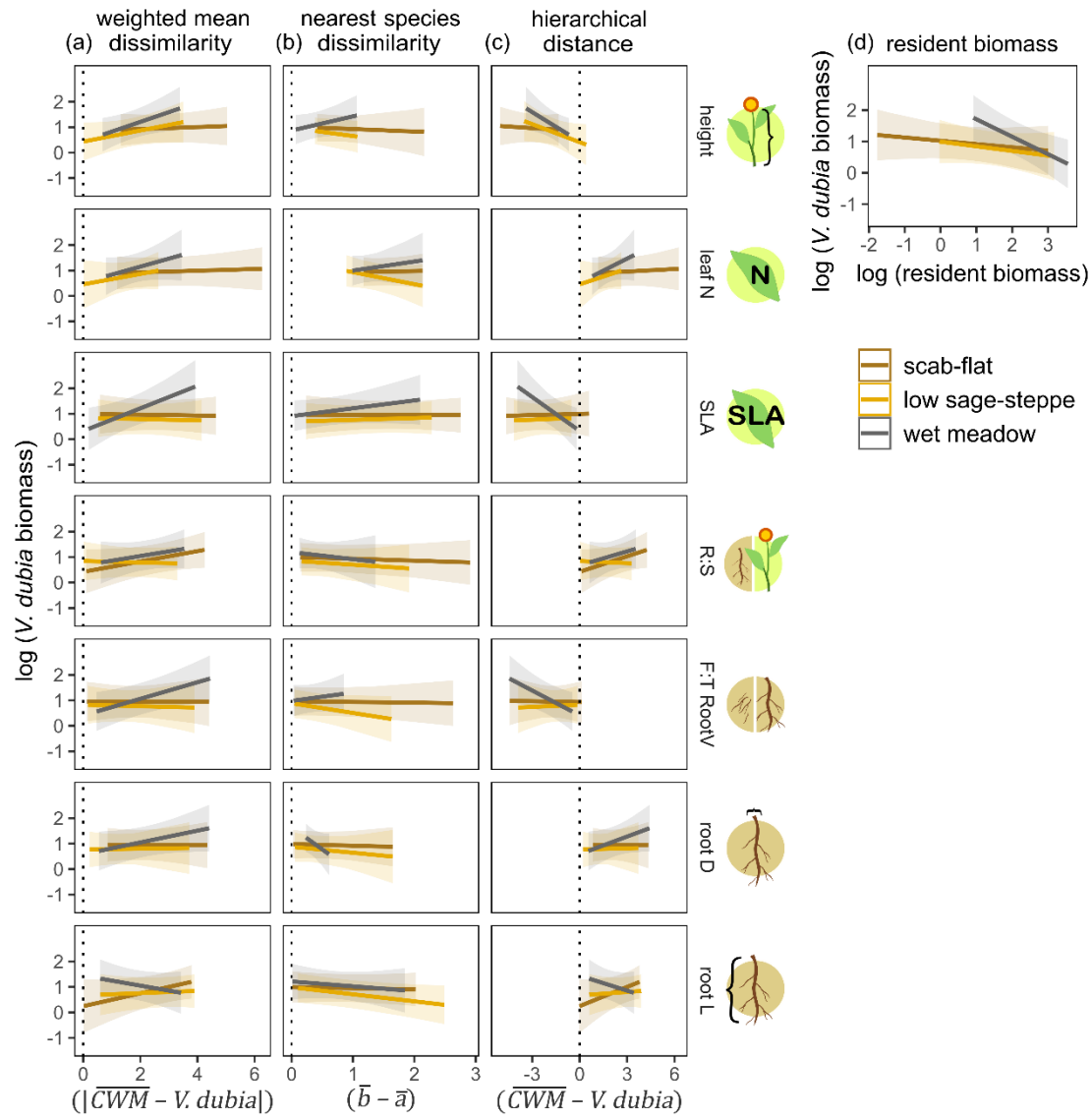


**Figure 3.2** Sampled communities were distributed across a productivity and soil moisture gradient consisting of three vegetation types: scab-flats, low sage-steppe, and wet meadows.



**Figure 3.3** Non-metric multidimensional scaling ordination of species in trait space.

*Ventenata dubia* (VEDU) is represented by a red point. Introduced annual grasses, *Bromus tectorum* (BRTE) and *Bromus arvensis* (BRAR5) are indicated by yellow points. Native species are represented by blue points. Points are scaled exponentially by their average foliar cover across all subplots. Species are represented by their USDA plant code (Table B.4.1).



**Figure 3.4** *Ventenata dubia* biomass response to (a) weighted mean dissimilarity, (b) nearest species dissimilarity, and (c) hierarchical distance community trait values and (d) resident biomass across three vegetation types spanning a productivity gradient. Estimates with 95% confidence bands.



### 3.9 Tables

**Table 3.1** Soil depth, soil moisture availability, mean foliar cover, mean resident biomass, and mean species richness for three vegetation types.

**Soils information are estimated from Ochoco National Forest soil categories and species associations from Paulson (1977). Mean foliar cover, resident biomass, and species richness are summarized from our study data (Appendix S2).**

	<b>Soil depth (cm)</b>	<b>Water-holding capacity</b>	<b>Foliar cover (%); (95% CI)</b>	<b>Resident Biomass (g); (95% CI)</b>	<b>Species richness; (min, max)</b>
<b>Ephemeral wet meadow</b>	50-150	Very low to moderate	53.9 (41.0, 70.9)	8.5 (4.8, 15.0)	9.0 (5, 16)
<b>Low sage-steppe</b>	39-45	very low to low	25.9 (19.6, 34.3)	4.1 (2.3, 7.2)	5.5 (3, 9)
<b>Scab-flat</b>	< 25	Very low	17.9 (13.4, 23.9)	1.9 (1.1, 3.4)	5.2 (3, 8)

**Table 3.2** Trait descriptions and abbreviations. (+) and (-) indicate direction of relationships between trait values and functions.

<b>Trait</b>	<b>Abbreviation</b>	<b>Description</b>	<b>Functional Significance</b>
<b>Height</b>	height	Height from soil surface to tallest photosynthesizing material <i>in situ</i>	Light interception (+) (Gaudet and Keddy 1988)
<b>Leaf nitrogen</b>	leaf N	Percent of nitrogen in leaf tissue	Photosynthetic rate (+) (Cornelissen et al. 2003)
<b>Specific leaf area</b>	SLA	Leaf area/ leaf mass (cm <sup>2</sup> /g)	High resource use and growth in herbaceous species (+) (Cornelissen et al. 2003)
<b>Root-to-shoot ratio</b>	R:S	Root mass/ shoot mass	Associated with stress tolerance (+) and resource allocation (Products et al. 2006)
<b>Fine-to-total root volume ratio</b>	F:T root V	Fine root volume/ total root volume	Reflects rate of nutrient uptake (+) (Roumet et al. 2006)
<b>Root diameter</b>	root D	Average root diameter (mm)	Reflects rate of nutrient uptake (-) (Roumet et al. 2006)
<b>Root length</b>	root L	Total length of roots (cm)	Associated with nutrient and water uptake (+) (Roumet et al. 2006)

## **CHAPTER 4**

### **FEEDING THE FIRE: ANNUAL GRASS INVASION FACILITATES SIMULATED FIRE SPREAD ACROSS AN INLAND NORTHWEST FOREST-MOSAIC LANDSCAPE**

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## Abstract

Invasive annual grasses are a growing global concern where they facilitate uncharacteristically larger and more frequent fires, particularly in desert, shrub-steppe, and savannah ecosystems. Forests of the western United States have remained relatively resistant to invasion by shade-intolerant annual grasses. However, where forests are adjacent to invaded areas, increased fire spread across ecotones could alter forest fire behavior and ecosystem resilience. In the Blue Mountains of eastern Oregon, forested ecosystems are highly heterogeneous, composed of a patchwork of forest and fuel-limited dwarf-shrublands and dry meadows that historically interrupted fire spread throughout the landscape. Recent invasion by the annual grass *ventenata* (*Ventenata dubia*) has increased fine fuel loads and continuity in non-forest patches, potentially altering landscape-scale fire behavior. Despite *ventenata*'s rapid spread across the Inland Northwest and growing management concern, little is known regarding how invasion influences fire within invaded areas or throughout the surrounding forest matrix. Here, we examine how invasion alters simulated fire across forest-mosaic landscapes throughout the 7 million ha Blue Mountains Ecoregion using the Large Fire Simulator (FSim).

We found that *ventenata* invasion increased simulated mean fire size, burn probability, and fire intensity throughout the ecoregion and the strength of these impacts varied by location and from landscape to ecoregional scales. Changes at the ecoregion-scale were relatively modest given that fine fuels increased in only 2.8% of the ecoregion where *ventenata* invaded fuel-limited vegetation types. However, strong localized changes were simulated within invaded patches (primarily dwarf-shrublands) and where invasion facilitated fire spread into and between nearby forests. Within invaded patches, burn probabilities increased by 45% and increased flame lengths would likely require fire management strategy to shift from hand tools to requiring large

machinery. Forests with 25% of their surrounding landscape invaded experienced a 28% increase in burn probability and 16% increase in the probability of high intensity crown fire when burned (flame lengths > 2.4 m). Increased canopy loss could have severe implications for forest resilience given that invasive annual grasses can heavily invade these early seral forests and limit post-fire forest recovery. Our study demonstrates how annual grass invasion can influence fire behavior and resilience across forest landscapes despite primarily invading non-forested areas, and highlights invasion as an important management issue in a forest-mosaic ecosystem.

#### **4.1 Introduction**

Invasive grasses are a growing global concern where they increase fine fuels and facilitate larger and more frequent fires in previously fuel-limited or fire-limited desert, shrub-steppe, savannah and forested ecosystems (D'Antonio and Vitousek 1992, Brooks et al. 2004, Kerns et al. 2020). In historically fire-resistant and resilient ecosystems, changes in fuels and fire regimes, including more frequent, uncharacteristic or severe fire, often result in the loss of fire-sensitive native vegetation and altered ecosystem function (D'Antonio and Vitousek 1992, Hessburg et al. 2005). Ecosystems that evolved with low to moderate severity and frequent fire, including many forests of the western United States have been relatively resistant to grass invasion (Martin et al. 2009, Rejmánek et al. 2013) and subsequent grass-fire feedbacks commonly known as “grass-fire cycles” (D'Antonio and Vitousek 1992). However, forests could become susceptible to invasion impacts if fires in invaded areas increase spread into and between adjacent forests, potentially altering landscape-scale fire regimes and post-fire regeneration (Kerns et al. 2020). While grass-fire cycles are well documented in many shrub-steppe and desert ecosystems (D'Antonio and Vitousek 1992, Keeley 2000, Brooks et al. 2004, 2016), there remains a gap in knowledge about how these species influence fire and ecosystem function in forest-mosaic landscapes composed

of forest and non-forest patches (Fusco et al. 2019). This information is critical for designing and implementing effective fuel and fire management strategies for grassy and woody fuels to promote landscape resistance and resilience.

The spatial arrangement of vegetation and fuels influence landscape-scale fire patterns and behavior. Landscapes with high heterogeneity (e.g. forest-mosaics) are generally considered as having slower fire spread rates and greater overall fire resistance than landscapes of homogeneous forest, given that non-forest portions of the mosaic are likely to have lower fuel loads and/or flammability, acting as natural fire breaks (Hessburg et al. 2005, Collins and Stephens 2007, Duguy et al. 2007, Parks et al. 2015). For example, the homogenization of forests as a result of fire suppression and forest encroachment into meadows and shrubland patches has been associated with more severe fires and increased landscape-scale fire spread (Hessburg et al. 2005). Alternatively, grassy non-forest patches could be considered to be fast, flammable fuels that may act as conveyor belts” for surface fire across the landscape (Hessburg et al. 2005). These principles are commonly applied to the placement of fuel reduction and fuel break treatments aimed at reducing fire hazard by fragmenting areas of continuous fuels to slow fire spread and reduce fire intensity (Finney 2001). While there has been much focus on the use of woody fuel treatments to mitigate wildfire size and severity and promote ecosystem resistance and resilience (Agee and Skinner 2005, Wei 2012, Prichard and Kennedy 2014, Prichard et al. 2020), there is little examination about how the spatial arrangement of invasion influences fire behavior in dry forests and forest-grass mosaics.

Positioned at the center of a recent annual grass invasion, the Blue Mountains Ecoregion (BME) of the Inland Northwest, U.S.A. presents an opportune place to investigate the impacts of grass invasion on fire in a forest-mosaic landscape. The landscapes that make up the BME are

highly heterogeneous and comprise a patchwork of forest interspersed with sparsely vegetated low productivity dry meadows and dwarf-shrublands locally known as “forest scablands”. These meadows and scablands are not forest capable and are maintained by extremely shallow soils rather than frequent low severity fire. Until recently, these areas were resistant to widespread grass invasion (Johnson and Swanson 2005). However, a recently introduced invasive annual grass, ventenata (*Ventenata dubia*), has heavily invaded many forest scablands (Tortorelli et al. 2020), where it increases fuel loading and continuity in previously fuel-limited patches within the forested mosaic (Gibson 2021). Much like the pervasive cheatgrass (*Bromus tectorum*) invasion across much of the American Great Basin (Brooks et al. 2004), ventenata grows in dense patches, has a high surface-area-to-volume ratio resulting in a quick-drying fuel that senesces earlier in the fire season than many native species and facilitates rapid fire spread. The potential for ventenata to alter fuels and fire behavior is substantial and contributes to its high management concern throughout the region (Hallmark and Romero 2015). Despite these concerns, the direct effects of the ventenata invasion on fire behavior within invaded areas and transmission across the surrounding landscape have yet to be measured.

In this study, we use a novel application of the large wildfire simulator (FSim) (Finney et al. 2011) to model the effects of annual grass invasion on fire spread, burn probability, and fire intensity throughout the 7 million ha Blue Mountains Ecoregion. A simulation-based study allows for extensive exploration of the effect of invasion on landscape-scale fire while holding all other factors (e.g. fire weather and ignitions) constant. We developed specific spatial fuel layers that captured the landscape (1) prior to invasion and (2) presently with the invasion that provided information for two simulations (uninvaded, and invaded). We then evaluated how the model output differed at local to landscape-scales and within different vegetation types for the

two simulations. Our aims were to characterize how *ventenata* and the spatial patterns of invasion alter simulated fire spread, burn probability, and flame lengths at multiple spatial scales including individual forest cells, continuous invaded patches, landscapes (~100 ha), and the entire ecoregion.

Invasion into historically sparsely vegetated forest openings (non-forest patches) and ecotones may impact fire resistance through multiple mechanisms and at different spatial scales, and this may have important implications for forest resilience. We predicted that invasion would dramatically increase ignitability and intensity in non-forest patches and facilitate fire spread across forest ecotones and into adjacent forests (Fig. 4.1). We expected the magnitude of fire impacts to vary depending on the spatial arrangement and extent of invaded patches within the larger forested mosaic, with greater shifts in burn probability and fire behavior in larger invaded patches, and in forested areas and landscapes with a high proportion of invasion in their immediate neighborhood.

## **4.2 Materials and Methods**

### ***4.2.1 Study area***

The study area is the 7 million ha Blue Mountain Ecoregion (BME) as defined in the EPA Ecoregion Level III (Fig. 4.2) (Omernik and Griffith 2014). The climate regime is temperate with precipitation and temperatures varying along topographic and elevational gradients. On average, the region receives between 27 and 57 cm of precipitation each year primarily falling between November and June. High temperatures average in the upper 20s °C and lows in the -10s °C (PRISM Climate Group 2019). Vegetation across the ecoregion is a highly variable mosaic of forest and non-forest vegetation types (Fig. 4.2). Closed and open canopy forests are



primarily composed of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) with increasing grand fir (*Abies grandis*) and western larch (*Larix occidentalis*) at higher elevations. Forested areas are commonly interspersed with lithic scabland soils on plateau uplands supporting sparsely vegetated dwarf-shrublands composed of scattered shallow-rooted bunchgrasses and, in many cases, low growing sagebrush species *Artemisia rigida* or *Artemisia arbuscula* (Fig. 4.2) (Johnson and Swanson 2005). More productive non-forest vegetation types include big sage-brush steppe concentrated in the west and southeast sections of the ecoregion, and perennial bunchgrass grasslands in the northeast corner of the ecoregion (Fig. 4.2). Closed and open canopy forest are the most prevalent vegetation types across the study area (collectively 51%); followed by dry shrubland, primarily big sagebrush-steppe (24%); herbaceous grassland (9%); dwarf-shrubland (7%); agriculture (3%); recently disturbed (2%); non-vegetated (2%); sparsely vegetated (1%); and wetland and riparian (1%) (Fig. 4.2; Appenidx C.1) (LANDFIRE 2019a).

#### ***4.2.2 Fuel characterization: creating custom landscapes***

To address our aims, we required two data layers representing landscape fuels (“fuelscapes”) for our simulations (“uninvaded” and “invaded”) that best represented the non-forest fuels associated with the study area without and with *ventenata*, respectively. We created the two custom fuelscapes based on modifications to the Landscape Fire and Resource Management Planning Tools (LANDFIRE) 2.0.0 fuel model grid (LANDFIRE 2019b) as described below. This version of LANDFIRE represents vegetation conditions for the end of 2016. It is customary to modify the LANDFIRE fuel model grids based on the availability of specific and improved local data and sources (Scott et al. 2012, 2016, Thompson et al. 2012). However, specific

modifications owing to grass invasion have never been attempted, therefore we detail below our novel fuelscape development.

The uninvaded fuelscape was created in two stages. First, we developed a core *ventenata* habitat layer to depict areas with historically low fuel loads where we expected the *ventenata* invasion to have the greatest impact on fuel load and structure. We selected vegetation types that (1) were historically relatively fire resistant with fine fuel loads less than 897 kg ha<sup>-1</sup>; (2) are generally not heavily impacted by other annual grass invasions, including cheatgrass; and (3) are at high risk for *ventenata* invasion given their vegetation associations (Jones et al. 2018, Tortorelli et al. 2020, Nietupski 2021). Vegetation types included in the vegetation layer were determined through discussions with ecologists, botanists, and weed managers. All core habitat types were combined into a single 120 m resolution raster in ArcGIS for the study area and a 30 km buffer, consistent with FSim model inputs. The core habitat layer covered 959,721 ha, 13.5% of the study region (Fig. 4.3). See Appendix C.2 for complete list of vegetation types included and additional methods.

We observed that the LANDFIRE fuel models (Scott and Burgan 2005) typically overestimated fuel loads and spread rates within the core habitat layer when uninvaded (see Gibson 2021). Therefore, we reassigned these areas to fuel models that more accurately reflected lower fuel loads prior to invasion based on our field observations, expert opinion, and herbage estimates (Johnson and Swanson 2005, Gibson 2021). Areas classified as fuel models GR2 (Low Load, Dry Climate Grass) were reclassified as GR1 (Short, Sparse Dry Climate Grass) and areas classified as GS2 (Moderate Load, Dry Climate Grass-Shrub) were reclassified as GS1 (Low Load, Dry Climate Grass-Shrub) (Table 4.1). The spatial arrangement of these fuels then served as our uninvaded fuelscape for analysis.

To create the invaded fuelscape, we reassigned fuel models from the uninvaded fuelscape to reflect higher fuel loads where *ventenata* had invaded within our core habitat layer (Fig. 4.3). Invaded areas were determined using a newly developed *ventenata* distribution map for the BME (Nietupski 2021). This map identified *ventenata* presence greater than 20% cover as estimated from land surface phenology, climate, and biophysical indicators derived from remotely sensed data (Nietupski 2021). *Ventenata* invaded 7.7% of the ecoregion according to these estimates, however we only reassigned fuel models in 2.8% of the study region (190,565 ha) where invasion overlapped low-productivity vegetation types represented in the core habitat layer. Fuel models were reassigned to represent increased fine fuel loading and spread rates in invaded areas, and where shrubs were present, a shift from woody to fine fuel driven fire behavior (Table 4.2) (Scott and Burgan 2005) based on our field observations, biomass estimates from invaded dwarf-shrublands (Gibson 2021), and discussions with experts. Vegetation types in areas where we reassigned fuel models were 58% dwarf-shrubland, 20% shrubland, 11% herbaceous/grassland, and 10% open tree canopy. The remaining 1% was spread between the remaining vegetation types discussed above.

#### ***4.2.3 Wildfire simulation modeling: the Large Fire Simulator (FSim)***

We used FSim (Finney et al. 2011) to simulate wildfire throughout the study area. FSim is a spatially explicit wildfire model that simulates the ignition, spread and suppression of large fires over thousands of years using a Monte Carlo style. FSim is described in detail elsewhere (Finney et al. 2011) as is its application to a diversity of spatial fuel management, planning, and risk analysis studies (Scott et al. 2017, Riley et al. 2018, Ager et al. 2019, 2020, McEvoy et al. 2021). Here, we briefly highlight its key features. FSim represents the landscape as a grid and proceeds at a daily time step. Daily fire weather conditions are randomly drawn from a temporally

autocorrelated distribution of conditions generated from observed daily weather records from a representative weather station (Grenfell et al. 2010). As FSim steps through each day of a year, fire ignition and spread may be simulated if the Energy Release Component (ERC) for the day exceeds the 80<sup>th</sup> percentile (Andrews et al. 2003). Ignition location is drawn from an ignition density grid, created from catalogue of recent observed ignitions. Fire spread is calculated using the minimum travel time (MTT) algorithm (Rothermel 1972, Finney 2002), and takes into account ERC, wind speed and topography. Suppression is simulated using an algorithm that determines the probability of daily containment using vegetation type, time since ignition, and fire behavior (Finney et al. 2009).

FSim outputs include: (1) raster grids of annual burn probability (BP), (2) the conditional probability of a pixel burning within six flame length classes, given that a fire occurs ( $CBP_i$ ), (3) a fire size list including the locations of ignitions for each simulated fire, and (4) shapefiles of all simulated fire perimeters. The BP for a given pixel is calculated as the number of times a pixel burns divided by the number of years in the simulation (here, 10,000).  $CBP_i$  are calculated from fireline intensity and take into account information about fuel moisture, wind, the direction from which fire encounters each pixel, (i.e. as heading, flanking, or backing fire) and their slope and aspect (Finney 2002). The six flame length classes are 0-0.6 m, 0.6-1.2 m, 1.2-1.8 m, 1.8-2.4 m, 2.4-3.7 m and >3.7 m. The sum of  $CBP_i$  adds to 1 for each pixel or 0 if the pixel never burned (e.g. in non-burnable areas).

We first ran FSim using the invaded fuelscape at 120 m resolution. We calibrated FSim to approximate the distribution of size and frequency of fires larger than 100 ha recorded in the USFS Fire Occurrence Database (FOD) from 2000 to 2017 (Short 2021), assuming these years reasonably represent the recent invasion footprint. Weather data were obtained from the Allison

remote automated weather station (RAWS, 43.92 °N, -119.59 °E), located within the study area (Fig. 4.2). Topography (slope, aspect, and elevation) and canopy data (canopy bulk density, base height, cover, and height) were extracted from LANDFIRE (LANDFIRE 2016), and aggregated from 30 m to 120 m resolution. We ran the simulation for 10,000 years and adjusted parameters so that mean fire size and number of fires fell within the 70% confidence intervals around observed values (Appendix C.3) (Scott et al. 2018). Average annual burn probability simulated by FSim was 0.0083, similar to the observed value (0.0087). For the uninvaded simulation, after FSim was calibrated using the invaded fuelscape, we simulated uninvaded conditions by simply replacing the invaded fuelscape with the uninvaded fuelscape, holding all other inputs constant.

## 4.3 Data analysis

### 4.3.3 Burn metrics: ecoregion scale

To represent a meaningful shift in fire intensity between the invaded and uninvaded simulations for estimating ecosystem effects and interpreting management outcomes, we calculated the conditional probability of each pixel burning at moderate and high intensity: flame lengths exceeding 1.2 m ( $CBP_{>1.2m}$ ) and 2.4 m ( $CBP_{>2.4m}$ ). We chose these thresholds because flame lengths above 1.2 m often require a shift in fire management and suppression practices from hand tools to large machinery or aerial retardant (Andrews and Rothermel 1982) and can lead to moderate increases in crown fire (NWCG 2006, Ager et al. 2014). Flame lengths exceeding 2.4 m often result in crown fire and can lead to tree mortality in dry mixed conifer forests depending on diameter and canopy base height (Ager et al. 2010, 2014). We also calculated the proportion of the study area that is likely to burn at moderate and high intensity fire (conditional on burning) for the uninvaded and invaded simulation by multiplying the study area (ha) by  $CBP_{>1.2m}$  and  $CBP_{>2.4m}$ . We primarily focused our analyses on shifts in  $CBP_{>1.2m}$  when summarizing *ventenata*

effects on fire behavior in non-forested areas (e.g. dwarf-shrublands), as these vegetation types lack tree canopies to carry fire.

To examine how invasion may influence burn metrics at the ecoregion scale, we compared the mean number of large fires ( $>100$  ha), fire size, BP,  $CBP_{>1.2m}$ ,  $CBP_{>2.4m}$  and area burned at moderate and high intensity between the uninvaded and invaded simulation for the entire ecoregion. We also calculated mean and median BP and  $CBP_{>1.2m}$  by vegetation type and for invasion-adjacent areas (3 km buffer around invaded patches and excluding invaded areas) and compared these between the two simulations. Absolute differences between invaded and uninvaded simulations (*invaded - uninvaded*) and proportional differences (*absolute difference / uninvaded*) were calculated for each vegetation type, for all areas where fuels were adjusted to represent invasion (“invaded core habitat”), and for the entire study area.

#### **4.3.2 Fire transmission**

To assess how ventenata invasion may influence large fire spread across the forest-mosaic, we compared fire transmission patterns in the invaded and uninvaded simulations. For each simulated fire perimeter, we recorded the vegetation type of the ignition cell and the area burned for each vegetation type within that fire perimeter using the ArcGIS tool box XFire (Kingbird Software 2018). From these data, we summarized mean area burned per year for each burned vegetation type by ignition vegetation type for both simulations. To focus analysis on large fires that were more likely to have spread and cross between vegetation types, we subset the data to include only fire perimeters from the uninvaded simulation that were  $>100$  ha. We included fires from the invaded simulation with corresponding ignitions. Fire perimeters that ignited outside of the study area (in the 30 km buffer) were removed prior to this analysis. In total, we analyzed 209,078 fire perimeters from each simulation.

### *4.3.3 Spatial patterns of fire: local forest, patch, and landscape scales*

We modeled the influence of invasion patterns on burn metrics at various scales including forest cells, patches of continuous invaded core habitat, and averaged across ~100 ha landscapes using generalized additive models (GAMs). GAMs are generalized linear models where the response variable depends on smooth functions of one or more predictor variables. This allows for the estimation and interpretation of nonlinear patterns that can be missed when fitting strictly linear models. Smooth functions balance goodness-of-fit and overfitting using a cross-validation approach (Hastie and Tibshirani 1987). All GAMs were fit with a cubic spline function and Gaussian family from the package “mgcv” (Wood et al. 2016).

We examined the effect of invasion on fire behavior in uninvaded forest cells by relating forest burn metrics to the proportion of invaded area within the surrounding neighborhood. Areas adjacent to invaded patches might be the most likely to show changes in fire behavior, and neighborhood analyses compliment an ecoregion-wide assessment. The focal forest cells were classified as the cell at the center of each 116.6 ha (1080 m x 1080 m, or 9x9 cells) neighborhood determined using a moving window. Only cells classified as uninvaded and forest (open or closed canopy) were included as focal forest cells. A neighborhood size of 116.6 ha was chosen to approximate the 100 ha fire size considered by FSim to constitute “large fires”. We developed separate GAMs to examine how BP,  $CBP_{>1.2m}$ ,  $CBP_{>2.4m}$  and the absolute differences in these burn metrics in forested cells were influenced by proportion of invasion (and corresponding uninvaded core habitat for the uninvaded simulation) in the surrounding neighborhood. We also fit models to demonstrate how burn probability and CBP differed when the corresponding core habitat areas were uninvaded. To narrow the sample size and focus the analysis on the effect of varying levels of landscape invasion, we included only areas where the proportion of

neighborhood invaded was greater than 0, resulting in a sample size of 357,182 focal forest cells and corresponding neighborhoods. Neighborhood calculations were performed using the “focal” function from the package “raster” (Hijmans 2020).

To investigate how the size of an invaded patch influenced within-patch fire behavior, we first calculated the average BP and  $CBP_{>1.2m}$  for each invaded patch ( $n = 17,783$ ) in the invaded simulation, and the same fire metrics for the corresponding core habitat areas when uninvaded for the uninvaded simulation. Second, we modeled the response of within-patch BP,  $CBP_{>1.2m}$ , and the absolute differences in these burn metrics to patch size (log hectares) using separate GAMs. Patch sizes were extracted using the function “extract\_lsm” from the package “landscapemetrics” with patches defined as invaded core habitat with connections in any of 8 directions (Hesselbarth et al. 2019). All spatial pattern analyses were conducted in R 4.0.4 (R Core Team 2021).

To examine how invasion influenced landscape-scale burn probability and fire behavior within heterogeneous forest-mosaic landscapes, we related BP,  $CBP_{>1.2m}$ ,  $CBP_{>2.4m}$ , and the absolute differences between the invaded and uninvaded scenario for these burn metrics to the proportion of invaded area within 116.6 ha landscapes. Landscape burn metrics were calculated as the average of each burn metric across the entire landscape using a moving window analysis from the package “raster” (Hijmans 2020). We developed separate GAMs to examine how the proportion of the invaded landscape (and corresponding uninvaded core habitat) influenced landscape BP,  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$ . We included only landscapes where the proportion invaded was greater than zero, as described above. In total 789,062 individual landscapes were analyzed.



## 4.4 Results

### 4.4.1 Burn metrics: ecoregion scale

At the ecoregion scale, the simulation using the invaded fuelscape resulted in more large fires and area burned, increased fire size, burn probability (BP),  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$  compared to the uninvaded simulation; however, many of these differences were relatively small (Table 4.3, Fig. 4.4). Of all the burn metrics examined, invasion had the greatest influence on mean annual area burned, increasing it by 2.6% relative to the uninvaded simulation (Table 4.3). More importantly, simulated invasion effects on burn metrics were markedly high within and adjacent to invaded core habitat areas (Fig. 4.4). Within invaded core habitat, where fuel models were altered to reflect invasion (2.8% of the entire study area), mean BP was 0.002 (44.7%) higher,  $CBP_{>1.2m}$  was 0.27 (61.8 %) higher, and  $CBP_{>2.4m}$  was 0.02 (39.0 %) higher in the invaded simulation. In invasion-adjacent areas (3 km invaded area buffer excluding invaded areas), BP was 0.0005 (5.9%) higher,  $BP_{>1.2m}$  was 0.009 (1.9%) higher, and  $BP_{>2.4m}$  was 0.002 (2.6%) higher in the invaded simulation. Open and closed tree canopy forest collectively made up 57.6% of the invasion-adjacent area.

Burn probability and fire intensity differed by vegetation type, as did the extent to which invasion influenced burn metrics (Fig. 4.5). Mean  $CBP_{>1.2m}$  by vegetation type ranged from 0.28 to 0.64 and mean BP ranged from 0.006 to 0.013. For both simulations, mean  $CBP_{>1.2m}$  was highest in wetland/riparian areas and closed canopy forests and lowest in recently disturbed areas (Fig. 4.5). Mean BP was highest in closed canopy forests for both simulations. The vegetation types with the lowest mean BP were dwarf-shrublands for the uninvaded simulation and recently disturbed areas for the invaded simulation (Fig. 4.5). As noted above, the effect of invasion on mean and median BP and  $CBP_{>1.2m}$  for most vegetation types appeared small at the ecoregion

scale (Fig. 4.5), however there was a substantial effect on burn metrics in dwarf-shrublands where the invasion was concentrated. Mean BP in dwarf-shrublands was 0.001 (15%) higher and mean  $CBP_{>1.2m}$  was 0.07 (14.0%) higher in the invaded simulation than in the uninvaded (Fig. 4.5).

#### ***4.4.2 Fire transmission***

Fire transmission between vegetation types differed between the invaded and uninvaded simulations (Fig. 4.6). On average, large fires ignited in dwarf-shrublands spread into and burned 13.7% (308 ha/yr) more of the study area in the invaded simulation. Collectively, these fires burned 14.5% (43 ha/yr) and 15.4% (72 ha/yr) more closed and open canopy forest respectively (Fig. 4.6, Appendix C.4). Simulated fires ignited in all vegetation types spread into and burned more dwarf-shrubland in the invaded simulation (Fig. 4.6, Appendix C.4). However, the greatest increases were from fires ignited in closed and open canopy forests which spread into and burned 16.5% (76 ha/yr) and 19.9% (132 ha/yr) more dwarf-shrubland in the invaded simulation, respectively. Self-burning in dwarf-shrublands (e.g. burned area from fires ignited within the same vegetation type) was 27.5% higher in the invaded simulation compared to the uninvaded simulation.

#### ***4.4.3 Spatial patterns of fire: local forest, patch, and landscape scales***

On average, burn metrics in forest cells were influenced by the amount of invaded area in the surrounding neighborhood (Fig. 4.7). Predicted difference in BP,  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$  in forested cells between the invaded and the uninvaded simulations increased substantially as the amount of invaded area within the surrounding 116.6 ha neighborhood increased (Fig. 4.7). With 25% of the neighborhood invaded, mean BP,  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$  in focal forested cells were 0.002 (28%), 0.045 (9%), 0.014 (16%) higher in the invaded simulation, respectively. These

differences increased when 50% of the neighborhood was invaded with mean BP,  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$  in focal forested cells measured 0.003 (58%), 0.091 (18%), and 0.029 (43%) higher, respectively. Using statistical models, invasion explained the greatest amount of variance in the absolute difference in forest BP ( $R^2 = 0.25$ ), followed by absolute difference in  $CBP_{>1.2m}$  ( $R^2 = 0.07$ ), and absolute difference in  $CBP_{>2.4m}$  ( $R^2 = 0.02$ ), respectively (Appendix C.5). In the uninvaded simulation, BP generally decreased in forested cells as the proportion of core habitat in their neighborhood increased; however, when these areas were invaded, BP remained relatively consistent regardless of increasing invasion in the neighborhood (Fig. 4.7a). While less pronounced, forest  $CBP_{>2.4m}$  in the uninvaded and invaded simulations responded similarly to BP to increasing neighborhood invasion (Fig. 4.7c). These trends were not consistent for  $CBP_{>1.2m}$  in forested cells, where predicted  $CBP_{>1.2m}$  increased substantially as the proportion of the neighborhood invaded increased in the invaded simulation, but remained relatively low when the corresponding core habitat was uninvaded (Fig. 4.7b). See Appendix C.5 for summary statistics for all GAMs.

The invaded fuelscape represented patches of continuous invaded core habitat ranging in size from 1.4 to 8,650 ha (i.e. 1 to 6,007 pixels). The median and mean invaded patch sizes were 1.4 and 10.7 ha respectively, with only a quarter of invaded patches measuring larger than 4.3 ha. Predicted BP and  $CBP_{>1.2m}$  were generally higher in invaded patches than when these same core habitat areas were uninvaded and the magnitude of this difference varied according to patch size (Fig. 4.8). With both BP and  $CBP_{>1.2m}$ , the difference between the invaded and uninvaded simulations increased as the size of the invaded patch increased (Fig. 4.8). Despite these trends, patch size explained a relatively small amount of variance in the absolute difference in BP ( $R^2 = 0.04$ ) or  $CBP_{>1.2m}$  ( $R^2 = 0.01$ ) between the invaded and uninvaded simulations (Appendix C.5).

Invaded patches had consistent BP regardless of patch size, but in these same core habitat patches when uninvaded, BP steadily decreased with increasing patch size (Fig. 4.8a). This suggests that patch size does not strongly influence BP given continuous fuels, but that uninvaded patches may act as barriers to fire spread reducing inner patch burning with increasing patch size. In contrast,  $CBP_{>1.2m}$  increased with increasing patch size in the invaded simulation, while  $CBP_{>1.2m}$  values for these same patches when uninvaded remained constant regardless of patch size (Fig. 4.8b). This could indicate that flame lengths are more sensitive to patch size than BP when fuels are continuous, and that invasion acts as the opposite of a fuel break by increasing fire spread and intensity. In the uninvaded simulation, predicted  $CBP_{>1.2m}$  remained consistently below 0.45 regardless of patch size, but ranged from 0.6 to 0.75 when the same patches were invaded, demonstrating that invaded patches are much more likely to experience flame lengths above 1.2 m when burned (Fig. 4.8b).

Landscape-scale burn metrics were heavily influenced by the proportion of the landscape invaded (Fig. 4.9). With 25% of the landscape invaded, predicted landscape BP,  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$ , were 0.002 (29%), 0.098 (21%), and 0.009 (16%) higher in the invaded than the uninvaded simulation, respectively. These differences increased when 50% of the landscape was invaded and BP,  $CBP_{>1.2m}$ , and  $CBP_{>2.4m}$  were 0.003 (54%), 0.184 (41%), and 0.021 (48%) higher in the invaded than the uninvaded simulation, respectively. The difference in predicted landscape BP between the invaded and uninvaded simulations increased with increasing proportion of the landscape invaded until the proportion invaded exceeded 80% (Fig. 4.9a). As invasion exceeded 80% of the landscape, the difference in landscape BP declined, likely because the core habitat has relatively low BP compared to forests. Whereas, the difference in landscape  $CBP_{>1.2m}$  and  $CBP_{>2.4m}$  generally increased as the landscape became saturated with invasion (Fig.

4.9b). Invasion best explained the variation in the absolute difference in landscape  $CBP_{>1.2m}$  ( $R^2 = 0.78$ ), followed by absolute difference in BP ( $R^2 = 0.42$ ) and  $CBP_{>2.4m}$  ( $R^2 = 0.37$ ), respectively (Appendix C.5).

## 4.5 Discussion

The extent to which the *ventenata* invasion influenced simulated fire in the Blue Mountains Ecoregion varied depending on the degree of invasion. As expected, the relatively small extent of reassigned fuel models reflecting invasion (2.8% of the entire ecoregion) resulted in modest shifts in fire behavior at the ecoregion scale. However, we saw substantial increases in burn probability and conditional probability of burning at moderate and high intensity with increasing invasion when considering smaller extents, including individual forest cells, non-forest patches, and landscapes (~100 ha). The greatest impacts to burn probability and conditional intensity occurred within large, invaded patches (primarily dwarf-shrublands) and nearby forests where increased fine fuel loads facilitated fire spread between dwarf-shrublands and the surrounding forested landscape. These results suggest that despite invading primarily non-forested patches, annual grass invasion can alter fire behavior and fire management practices across forest-mosaic landscapes where invasion serves as a vector connecting areas of higher fuel loads.

### *4.5.1 Invaded dwarf-shrublands heavily impacted*

As expected, *ventenata* was most concentrated and had the greatest impact on fire in dwarf-shrublands where increased fine fuel loading resulted in higher burn probability and conditional intensity. Our findings closely reflect those from observational studies in other western shrub and desert ecosystems with historically infrequent and patchy fire, where invasive grasses increased

area burned, fire frequency, and intensity in invaded areas (Balch et al. 2013, Bradley et al. 2017, Fusco et al. 2019).

Dwarf-shrublands support a diverse floral community with many rare and endemic species, and provide important habitat for wildlife, including endangered sage-grouse, and winter forage for elk and deer (Johnson and Swanson 2005). Increased burn probability may lead to shortened fire return intervals and altered fire regimes in invaded areas given that, like many invasive grasses, *ventenata* is known to recover quickly after fire (Tortorelli et al 2020). Such “grass-fire-cycles” can functionally remove established native species and regenerating seedlings that are not adapted to survive or recover quickly after fire, leading to state-shifts and the loss of ecosystem functions including hydrologic and nutrient cycling, wildlife habitat, and soil stability (D’Antonio and Vitousek 1992, Nagy et al. 2021).

Across the forest-mosaic, invasion impacts increased with increasing patch size, suggesting that larger invaded areas (primarily dwarf-shrublands) may be at higher risk for altered fire regimes and potential type-conversions. This is consistent with studies examining the effectiveness of woody fuel treatments on modeled fire behavior that found treatment size and the proportion of interior area to edges to be an important factor influencing exposure to fire (Finney et al. 2005, Arkle et al. 2012, Prichard and Kennedy 2014, Prichard et al. 2020). However, in this case, uninvaded patches acted as natural fuel treatments, buffering fire sensitive vegetation from the surrounding forested matrix and slowing landscape fire transmission, whereas invaded patches enhance fire flow and intensity.

#### ***4.5.2 Invasion facilitates landscape-scale fire spread***

Invasion in non-forest patches facilitated fire spread across the landscape, with increased fire transmission primarily occurring into and between forested areas. These findings reflect

observational and simulation studies in other ecosystems demonstrating that invasive grasses can contribute to fire spread between invaded and uninvaded vegetation types (Balch et al. 2009, Ellsworth et al. 2014, Gray and Dickson 2016). For example, patches of cheatgrass contributed to simulated landscape-scale fire spread across a mixed pinyon-juniper woodland and shrub-steppe landscape (Gray and Dickson 2016). Within the 48,500 ha northern Arizona study area, increased fire spread led to higher burn probabilities and conditional high intensity fire in nearby woodlands, and these increases were directly related to the amount of invasion in the surrounding area (Gray and Dickson 2016). Woodlands and shrublands with high proportions of invasion in their surrounding neighborhood (e.g. ecotones) were more likely to burn and, if exposed to fire, were more likely to burn at high intensity than when nearby core habitat patches were uninvaded.

Within the extensive Blue Mountains Ecoregion simulated in our study, even moderate invasion of the surrounding landscape (e.g. 20%) increased landscape-scale burn probability and conditional intensity compared to the uninvaded landscape. Our findings reflect those from fuel-reduction treatment studies where treatments reduced modeled landscape-scale fire occurrence and fire intensity with relatively low proportions of the landscape treated (Ager et al. 2010, Moghaddas et al. 2010, Collins et al. 2011, 2013). These results demonstrate the ability of the *ventenata* invasion to influence landscape-scale burn probability and fire behavior despite primarily invading non-forested areas and a relatively small proportion of the ecoregion. This is especially alarming given that *ventenata* has yet to meet its full invasion potential, and is predicted to become more abundant throughout the study area and across the American West (Jones et al. 2018, Jarnevich et al. 2021). Additionally, we did not consider the effects of *ventenata* on fuel or fire behavior where it invades more productive grasslands, shrublands, or

open canopy forests, nor where cheatgrass invasion was likely to have already altered fuel loads. Despite these vegetation types supporting more abundant fine fuels than dwarf-shrublands, higher fine fuel loads owing to *ventenata* invasion could increase flammability and continuity, further altering fire behavior across the region.

Increases in burn probability and fire frequency could have different ecological implications for forests than historically fire-resistant vegetation types. Given that many forests are in a state of fire deficit, more frequent low-severity fire may have desirable forest health outcomes including robust and diverse native herbaceous vegetation and thinning of smaller trees and species less tolerant of fire (Agee 1993, Hessburg et al. 2015). However, our results suggest that invasion may contribute to increased high intensity fire in nearby forests which could result in higher amounts of canopy loss when burned (Ager et al. 2010, 2014). In addition, fire effects owing to uncharacteristic fuels such as annual grasses may negatively impact understory native plant communities in early seral post-fire forests similar to effects documented in non-forested areas (Peeler and Smithwick 2018, Reilly et al. 2020, Tortorelli et al. 2020).

Even moderate reductions in canopy cover can create suitable conditions for annual grass invasion in forests, potentially expanding invasive annual grass distributions and exacerbating annual grass impacts (Peeler and Smithwick 2018, Kerns et al. 2020, Reilly et al. 2020). For example, *ventenata* is known to invade forests with up to 40% canopy cover and has heavily invaded burned forests following canopy loss (Tortorelli et al. 2020, Nietupski 2021). Fire-induced canopy reductions to under 30% promoted cheatgrass invasion in a Californian montane forest (Peeler and Smithwick 2018). Aside from fuel changes, invasive species can also limit forest recovery if tree seedlings are outcompeted by invasive species that readily colonize after fire even if climate and site conditions are favorable for establishment (Davis et al. 1998, Flory et



al. 2015). Competitive effects may be intensified by drought stress, either exogenous or from dry post-fire conditions if invasives are more tolerant than regenerating tree seedlings (Welles and Funk 2020). This may be especially problematic for forest edges which already exist in less suitable climate conditions (Parks et al. 2019), adding to concerns about transformations after high severity fire in forest ecosystems (Parks et al. 2019, Coop et al. 2020, Krosby et al. 2020).

Climate change is likely to exacerbate invasion-fire dynamics in many forest types. Low-elevation, dry, open forests that experience more frequent fire are currently at the highest risk for invasion (Crawford et al. 2001, Peeler and Smithwick 2018) and subsequent type conversions (Parks et al. 2019, Coop et al. 2020, Syphard et al. 2022). However, these conditions are predicted to expand as temperatures rise and precipitation becomes more variable (Davis et al. 2020). Furthermore, climate change is expected to lengthen fire seasons and increase disturbance activity across western forests (Abatzoglou and Williams 2016, Westerling 2016). This could include higher proportions of high severity fire in forests which may provide favorable conditions for invasion (Reilly et al. 2020) and short interval reburns (Kerns et al. 2020). Increased drought and fire in future landscapes may further facilitate invasion-fire feedbacks and lead to landscape-scale state shifts from forests to annual grasslands (Kerns et al. 2020). Future modeling work may consider investigating these ideas by combining state-and-transition, fire, and climate models as with the landscape model Envision (Bolte et al. 2006, Spies et al. 2017, Barros et al. 2018) or LSim (Ager et al. 2017) which integrates FSim fire modeling with the Forest Vegetation Simulator (FVS) (Crookston 2014).

#### ***4.5.3 Management implications***

Increased burn probabilities and intensity as a result of invasion may influence fire and fuel management strategies throughout the ecoregion, and more broadly. The loss of fire-resistant

patches from forest-mosaics could limit firefighter access points and safety zones (Hallmark and Romero 2015) and higher flame lengths may require additional and/or different resources to manage, thus limiting resources elsewhere. In invaded dwarf-shrublands, fires were likely to transition from low up to moderate intensity when burned (flame lengths exceeding 1.2 m) regardless of patch size. This increase would require a shift in fire management and suppression practices from persons using hand tools to large machinery or aerial retardant (Andrews and Rothermel 1982). Shifts in fire suppression strategies in forests were less likely, given that wildfires in forests generally have higher flame lengths than shrublands. However, forests in the vicinity of invaded areas may still experience shifts from moderate to high intensity fire in some cases. Such shifts, even if in relatively small areas, could put additional pressure on already limited equipment and human resources, further complicating fire management practices. Additionally, introducing machinery into invaded areas increases opportunities for propagules to spread into uninvaded areas, potentially exacerbating invasion and future impacts (Brooks 2008). Finally, increased ignitability of non-forest patches due to an abundance of highly flammable fuels, frequently occurring close to roads, could result in an increase in the number of lightning and human ignitions that grow into fires requiring management decisions (Fusco et al. 2019).

Thinning of forests through mechanical treatments and/or fire is a common management objective for creating and maintaining resilient forest structure in western dry conifer forests (Agee and Skinner 2005, Hessburg et al. 2015). While our study did not investigate the influence of fuel treatments on fire *per se*, many parallels can be drawn between abundance and configuration of grass invasions to studies examining the effectiveness of woody fuel treatments on modeled fire occurrence and behavior in forests. Reduction of fine fuels within non-forest patches (represented by the uninvaded fuelscape) may have similar effects to treating woody

fuels across a forested landscape. For example, many woody fuel reduction studies in western forests reported substantial decreases to simulated burn probability and potential flame lengths within treated areas, but the effects of treatment diminished as the proportion of the landscape treated decreased and fewer fires intersected the treated area (Moghaddas et al. 2010, Collins et al. 2011, Thompson et al. 2013, 2017). In a simulation study in northern California with nearly 10% of the landscape treated, fuel treatments reduced burn probability over 60% in treated areas and between 17% and 36% in nearby untreated areas (Moghaddas et al. 2010). Additionally, crown fire was reduced within treated areas, but these effects did not extend to the surrounding landscape (Moghaddas et al. 2010). These findings are comparable to results from our study, where burn probability and conditional intensity were 45% and 39% higher within invaded areas, respectively but varied considerably within uninvaded (i.e. untreated) areas depending on the extent of nearby invasion. Grass invasions are erasing the natural fuel treatments provided by low-productivity non-forested areas in forest-mosaic.

Incorporating weed management practices as fuels treatments could help meet management objectives in invaded forests, along forest ecotones, and in forest-mosaics where fires are likely to ignite in invaded areas and spread into/between adjacent forests. It is important to note that the duration and effectiveness of weed-oriented herbicide treatments without intensive restoration efforts is relatively short (e.g. 1-4 years) (Elseroad and Rudd 2011), whereas woody fuel treatment effectiveness often lasts over 5 years (Kalies and Yocom Kent 2016, Prichard et al. 2020). Invasive grassy fuels management requires increased focus in areas where natural fuel breaks have been compromised and fire management strategies have been altered due to invasion.

## 4.6 Conclusions

Our study is the first large scale ecoregional analysis of the impact of an invasive annual grass on simulated fire behavior in forest ecosystems and demonstrates that annual grass invasion can influence landscape-scale fire, despite primarily invading non-forested patches. Substantial increases in burn probability and conditional intensity within invaded areas and nearby forests due to increased fire spread may lead to shifts in fire suppression practices, tax already limited resources, and impact native plant communities and wildlife habitat. Grass invasions could have implications for forest and biodiversity loss as forest patches become surrounded by invasion and post-fire forest recovery is inhibited by competitive grasses. Additionally, given that invasion and fire are expected to be exacerbated by climate change, we expect these issues to become increasingly prominent in the future. While our study focused on a single species invasion in the inland Northwest, we hope to set the stage for additional work focused on the impacts of invasive species on fuels and fire behavior at landscape scales. In addition, results from our simulations can be applied to better understand what and how human and natural resources, such as communities and the wildland urban interface, at-risk species, water sources, soils, and other Highly Valued Resources or Assets (HVRAs) may be affected by invasion and altered fire behavior.

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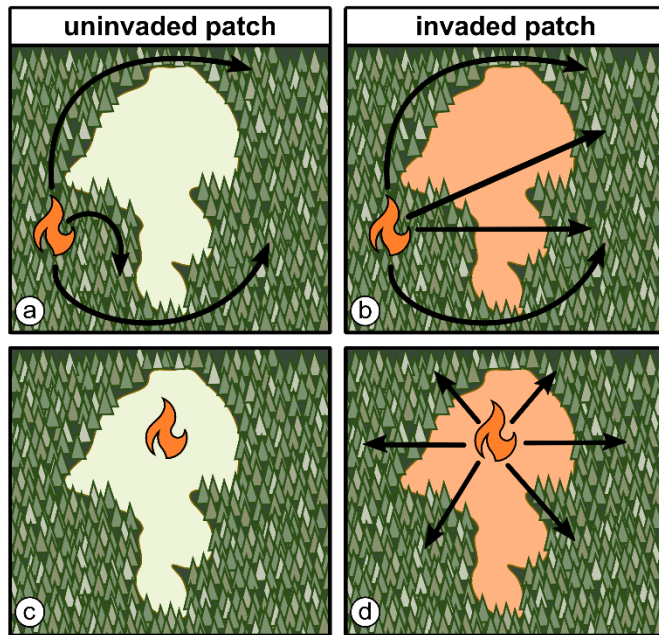
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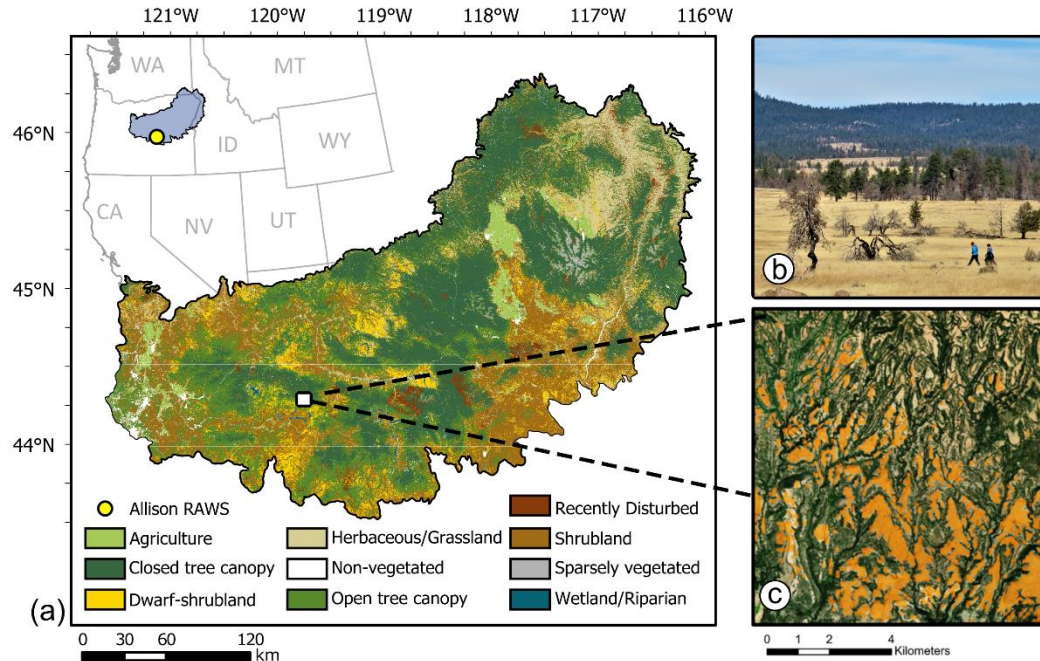
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## 4.8 Figures



**Figure 4.1** Predicted differences in the spatial arrangement of vegetation and fuels associated with grass invasion can influence landscape-scale fire patterns and behavior.

Panels (a) and (b) illustrate differences in fire spread when a fire is ignited in the forest and travels either (a) around the uninvaded non-forest patch or (b) across the invaded non-forest patch into the adjacent forest. Panels (c) and (d) illustrate fire behavior differences when a fire is ignited within the patch. (c) Fire fails to spread into the surrounding forest because the uninvaded patch lacks a continuous fuel bed. (d) Fire readily spreads across invaded patch and into surrounding forest.



**Figure 4.2** Vegetation map and photos of Blue Mountains Ecoregion

Panel (a): Blue Mountains Ecoregion mapped by vegetation type (modified from LANDFIRE 2.0.0 Existing Vegetation Type). Panel (b) depicts a forest-mosaic landscape following the 2015 Corner Creek fire where fire spread through invaded dwarf-shrublands into forested stringers and the surrounding forest matrix. Panel (c): Aerial imagery displaying the forest-mosaic landscape with invaded areas shaded orange (Nietupski 2021).

## 4.9 Tables

**Table 4.1** Total coverage (ha) of fuel models across the BME for LANDFIRE off-the-shelf data, the uninvaded fuelscape, and the invaded fuelscape that were reassigned based on core ventenata habitat and the ventenata map.

Percentages represent the percent of the total study area comprised by each fuel model.

<b>Fuel Model</b>	<b>Description</b>	<b>LANDFIRE 2019 (ha)</b>	<b>Uninvaded fuelscape (ha)</b>	<b>Invaded Fuelscape (ha)</b>
NB9	Bare ground	77,616 (1.1%)	77,616 (1.1%)	77,233 (1.1%)
GR1	Short, Sparse Dry Climate Grass	317,452 (4.5%)	430,822 (6.1%)	402,155 (5.7%)
GR2	Low Load, Dry Climate Grass	608,082 (8.6%)	494,712 (7.0%)	523,763 (7.4%)
GS1	Low Load, Dry Climate Grass-Shrub	687,838 (9.7%)	1,168,500 (16.5%)	1,052,893 (14.9%)
GS2	Moderate Load, Dry Climate Grass-Shrub	2,117,559 (29.9%)	1,636,897 (23.1%)	1,799,004 (25.4%)
SH1	Low Load Dry Climate Shrub	11,281 (0.2%)	11,281 (0.2%)	10,200 (0.1%)
SH2	Moderate Load Dry Climate Shrub	214,885 (3.0%)	214,885 (3.0%)	169,466 (2.4%)
TU1	Low Load Dry Climate Timber-Grass-Shrub	197,005 (2.8%)	197,005 (2.8%)	197,214 (2.8%)
TL3	Moderate Load Conifer Litter	535,552 (7.6%)	535,552 (7.6%)	535,343 (7.5%)

**Table 4.2** Within the ventenata core habitat area fuel models were reclassified to represent increased fine fuel loading and fire spread rates in invaded areas within the ventenata core habitat as represented below.

For example, areas classified as NB9 in the uninvaded fuelscape were reclassified as GR2 in the invaded fuelscape.

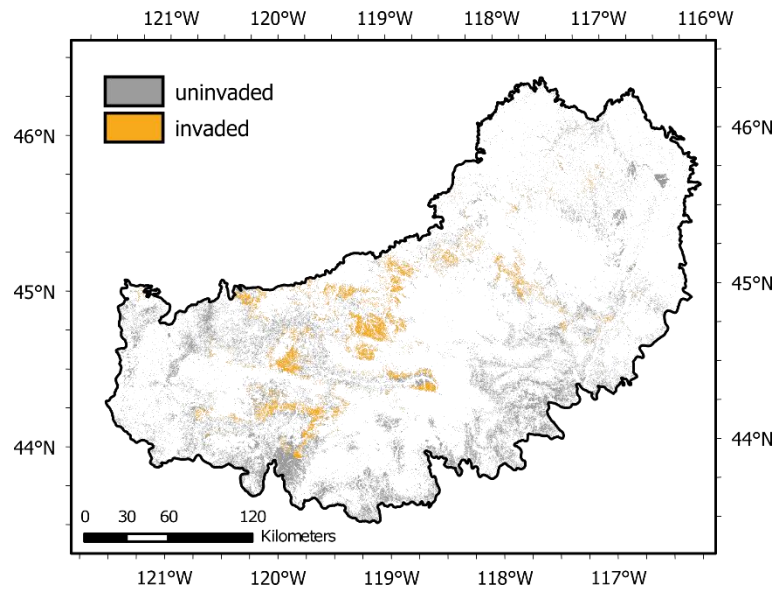
Uninvaded fuelscape		Invaded fuelscape	
NB9	<b>Bare ground</b>	→	<b>GR2 Low Load, Dry Climate Grass</b>
GR1	<b>Short, Sparse Dry Climate Grass</b>	→	<b>GR2 Low Load, Dry Climate Grass</b>
GS1	<b>Low Load, Dry Climate Grass-Shrub</b>	→	<b>GS2 Moderate Load, Dry Climate Grass-Shrub</b>
SH2	<b>Moderate Load Dry Climate Shrub</b>	→	<b>GS2 Moderate Load, Dry Climate Grass-Shrub</b>
SH1	<b>Low Load Dry Climate Shrub</b>	→	<b>GS2 Moderate Load, Dry Climate Grass-Shrub</b>
TL3	<b>Moderate Load Conifer Litter</b>	→	<b>TU1 Low Load Dry Climate Timber-Grass-Shrub</b>



**Table 4.3** Summary of burn metrics for the invaded and uninvaded simulations. All values report the mean for the entire ecoregion including all vegetation types.

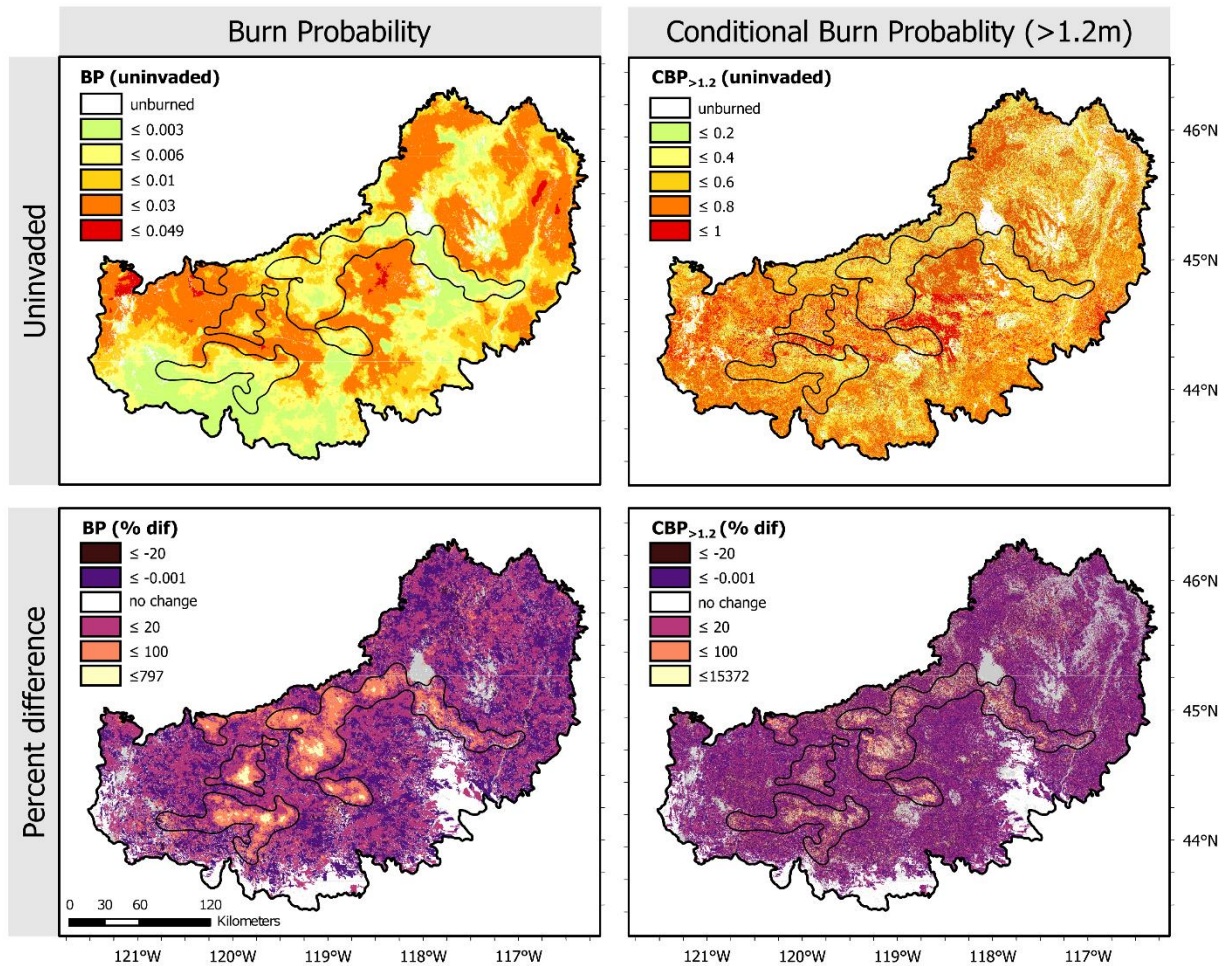
Absolute difference = invaded – uninvaded. Percent difference = absolute difference/uninvaded\*100. CBP<sub>>1.2m</sub> and CBP<sub>>2.4m</sub> indicate the area of the ecoregion that, if burned, would have flame lengths >1.2 m and >2.4 m, respectively.

	<b>Annual no. large (&gt;100 ha) fires</b>	<b>Annual area burned, ha</b>	<b>Fire size, ha</b>	<b>BP (range)</b>	<b>CBP<sub>&gt;1.2m</sub>, ha (% of ecoregion)</b>	<b>CBP<sub>&gt;2.4m</sub>, ha (% of ecoregion)</b>
<b>Invaded simulation</b>	25.9	78,199	3,017	0.009 (0-0.050)	3,697,106 (54.9%)	748,102 (11.1%)
<b>Uninvaded simulation</b>	25.7	76,220	2,968	0.009 (0-0.049)	3,622,070 (53.8%)	737,993 (11.0%)
<b>Absolute difference</b>	0.2	1,979	49	0.0002	75,035	10,109
<b>Percent Difference</b>	0.8	2.6	1.7	2.2	2.1	1.4



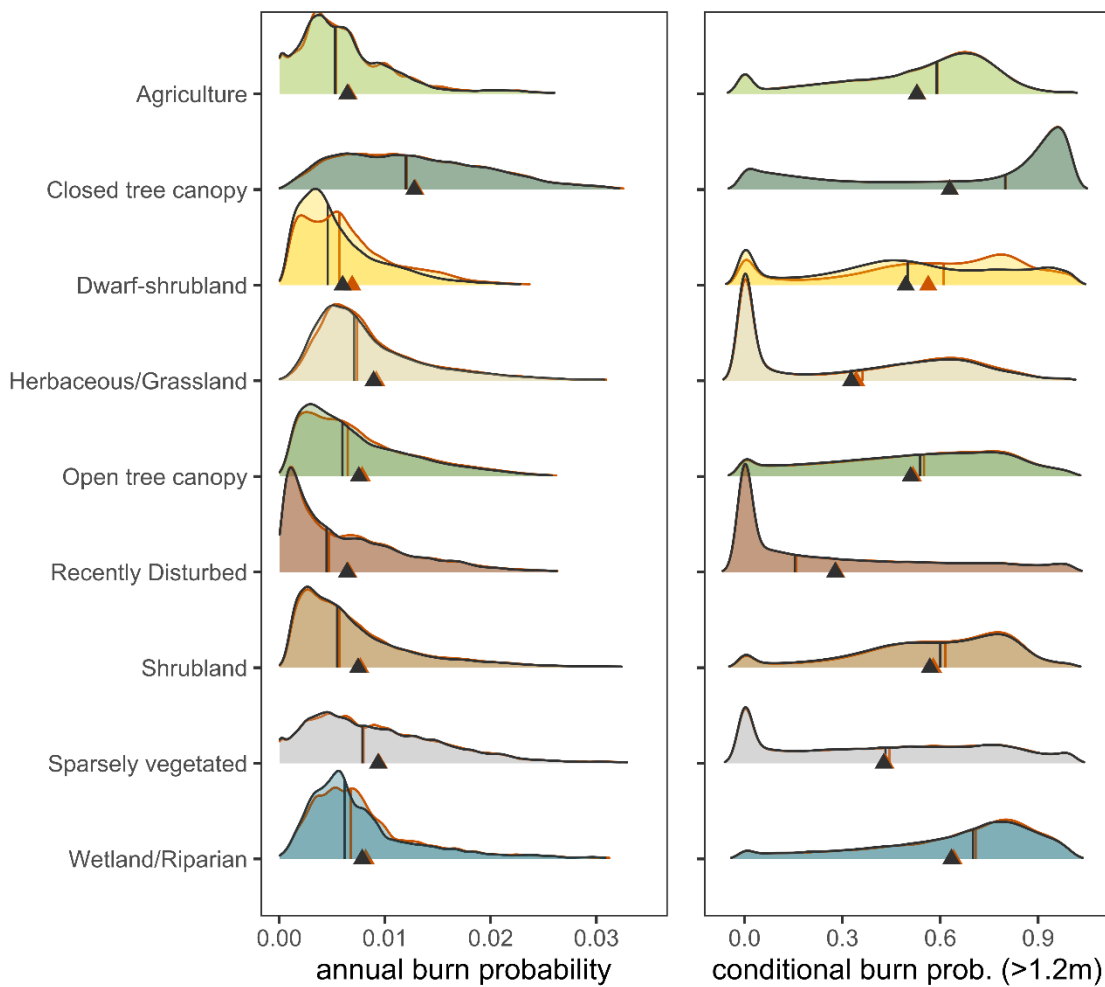
**Figure 4.3** The sparsely vegetated core habitat layer

This map shows areas where fuel models were reassigned to represent invasion in the invaded simulation (orange) according to the *ventenata* invasion map (Neitupski 2021) and core habitat that remained uninvaded in the invaded simulation (grey).



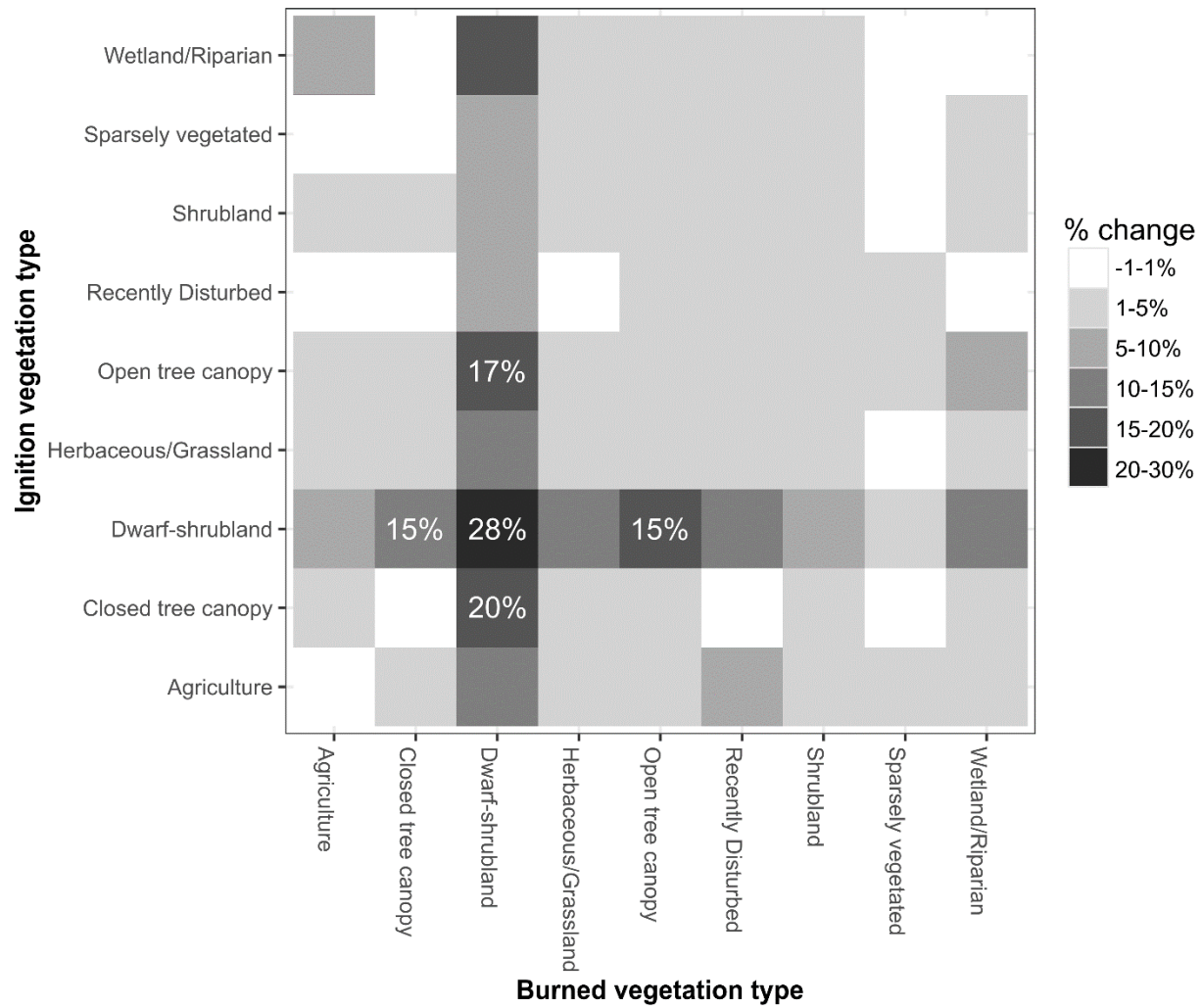
**Figure 4.4** Simulated annual burn probability (BP) and conditional probability of burning with flame lengths greater than 1.2m (CBP<sub>>1.2m</sub>) for the uninverted simulation and percent difference in fire metrics between the invaded and uninverted simulations ((invaded – uninverted)/uninverted\*100).

Positive values show where fire metrics increased with invasion and negative values represent where fire metrics decreased with respect to the uninverted simulation. Grey shading indicates non-burnable areas. Black polygons outline areas where invasion and reassigned fuel modes presented in Fig. 3 are concentrated.

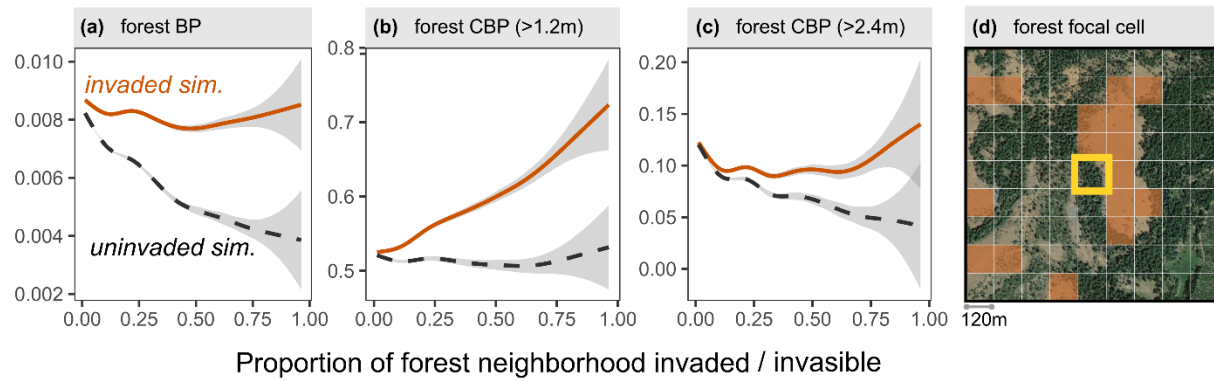


**Figure 4.5** Probability density plots of annual burn probability and conditional probability of burning at > 1.2 m flame lengths for the uninverted (black outline) and inverted (orange outline) simulations for each vegetation type.

Triangles represent the mean values and vertical lines represent median values for the uninverted (black) and inverted (orange) simulations.

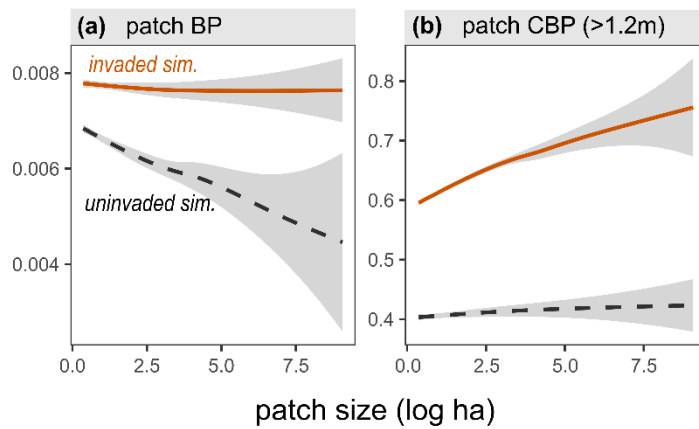


**Figure 4.6** Percent change in mean annual area burned between the invaded and uninvaded simulations (absolute difference / uninvaded\*100) for fires that started within “ignition” vegetation types and spread into “burned” vegetation types.



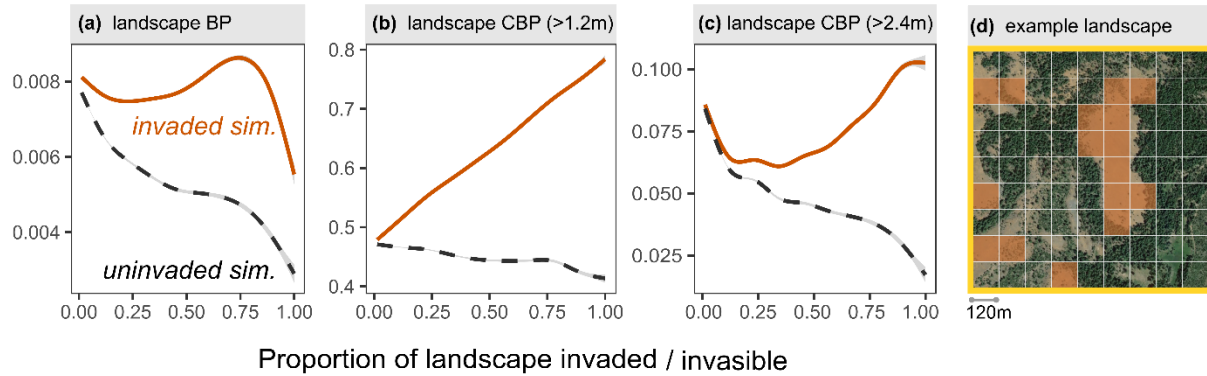
**Figure 4.7** Results from forest neighborhood analysis

Predicted focal forest (a) annual burn probability (BP), (b) conditional probability of burning with flame lengths >1.2 m ( $CBP_{>1.2m}$ ), and (c) conditional probability of burning with flame lengths >2.4 m ( $CBP_{>2.4m}$ ) response to the proportion of invaded neighborhood (with respect to the invaded simulation) surrounding forested focal cells ( $n = 357,182$ ). For example, with 25% of the neighborhood invaded, mean BP was 0.002 higher than in the same forested cell when the neighborhood was uninvaded. Panel (d) displays an example focal forest cell (outlined in yellow) and 116.6 ha neighborhood with invaded cells shaded orange.



**Figure 4.8** Results from patch size analysis

Predicted patch (a) annual burn probability (BP) and (b) conditional probability of burning with flame lengths  $>1.2$  m ( $CBP_{>1.2m}$ ) for invaded core habitat patches and corresponding areas in the uninvaded simulation in response to patch size ( $n = 17,783$ ). For example, with a patch size of 2.5 log ha (12 ha), mean patch BP was 0.0014 (23%) higher than in the same patch when uninvaded.



**Figure 4.9** Results from landscape analysis

Predicted landscape **(a)** annual burn probability (BP), **(b)** conditional probability of burning with flame lengths  $>1.2$  m ( $CBP_{>1.2m}$ ) and **(c)** conditional probability of burning with flame lengths  $>2.4$  m ( $CBP_{>2.4m}$ ) response to the proportion of landscape invaded and corresponding uninvaded core habitat areas in the uninvaded simulation. Landscape burn metrics were averaged across a 116.6 ha landscape ( $n = 789,062$ ). For example, when 25% of the landscape was invaded, mean BP was 0.002 higher than when the same landscape was uninvaded. Panel **(d)** displays example landscape with invaded cells shaded orange.



## CHAPTER 5 CONCLUSION

Understanding the drivers and impacts of invasive species is critical for developing effective management strategies to curb ecological and economic losses. This dissertation sought to characterize the biotic and environmental drivers of the rapidly spreading invasive annual grass *V. dubia* across the invasion front, the Blue Mountains Ecoregion, and evaluate its potential impacts on fire regimes and plant community composition and structure.

In Chapter 2, I characterized *V. dubia*'s novel niche, and investigated how invasion and wildfire may influence plant community composition and structure. *Ventenata dubia* generally invaded higher elevation sites than either *Bromus tectorum* or *Taeniatherum caput-medusae* and was most commonly associated with forest scabland vegetation and basalt-derived lithosols, although it also co-occurred with other annual grasses at lower elevations and on sandstone-derived soils. The three invasive annual grasses most commonly occurred together in severely burned forests where post-fire canopy loss and increased resource availability may facilitate invasion. However, unlike the other two grasses, *V. dubia* was not as strongly associated with burned areas and heavily invaded with and without visible disturbance. *Ventenata dubia* was weakly related to species diversity in unburned areas, but diversity decreased substantially with increasing invasion in burned sites. This suggests that *V. dubia* may fill in gaps around existing species and occupy a relatively empty niche in unburned areas while competitively excluding functionally similar species after fire by more readily utilizing post-fire resources. My findings demonstrate that *V. dubia* expands the overall invasion footprint of annual grasses in the region by invading areas that were historically resistant to other invasive annual grasses and indicate that *V. dubia* may outcompete functionally similar species following fire, resulting in lower community diversity in burned areas.

In Chapter 3, I expanded on our findings from Chapter 2 with an *in-situ* seed addition experiment to test how plant community composition and functional traits contributed to invasion resistance in three distinct vegetation types. Overall, scab-flat, low sage-steppe, and ephemeral wet meadow communities of the Blue Mountains Ecoregion were highly susceptible to *V. dubia* invasion regardless of trait composition or total biomass. However, communities with higher biomass in the most productive sites, wet meadows, demonstrated the greatest resistance to invasion. In the least productive sites, I did not find evidence that biomass facilitated invasion through the amelioration of abiotic stress as I predicted following the stress-gradient hypothesis (Bertness and Callaway 1994, Hacker and Gaines 1997). Of the seven above and below-ground traits I examined, specific leaf area, height, and fine-to-total root volume were the best predictors of invasion resistance in wet meadows. My results demonstrate how community traits and site productivity interact to influence community resistance to invasion and highlight that communities with high biomass and functional similar species to *V. dubia* may be more resistant to invasion. These findings could have important implications for predicting community resistance to invasion and for choosing species with which to restore invaded communities.

Results from Chapter 3 inspired an additional study investigating how above-ground biomass removal influenced *V. dubia* success in the same three vegetation types published in *Biological Invasions* (Tortorelli et al. 2022). I found no effect of above-ground biomass removal on *V. dubia* abundance in this study, suggesting that microsite differences or below-ground interactions may be more important predictors of invasion than competition or facilitation occurring above ground.

Chapter 4 examined the extent to which the *V. dubia* invasion influences simulated fire occurrence and fire behavior within invaded dwarf-shrublands and across forest-mosaic

landscapes of the Blue Mountains Ecoregion using the Large Fire Simulator (FSim) (Finney et al. 2011). Invasion most strongly influenced fire occurrence and flame lengths in dwarf-shrublands – the vegetation type where the invasion was concentrated. However, increased fire transmission between invaded non-forest patches and adjacent forests increased fire occurrence and the probability of experiencing high intensity fire in forested areas and across forest-mosaic landscapes. The difference in burn probability and intensity between invaded and the uninvaded fire simulation increased with increasing invasion in the surrounding area. These findings demonstrate how invasion can influence fire occurrence and behavior across a forest-mosaic landscape and highlights annual grass invasion as a potential management issue in a dry forest ecosystem.

Collectively, these chapters provide some of the first characterization of *V. dubia*'s niche and invasion dynamics, and detail how this invasion differs from other invasive annual grasses throughout the region. I demonstrate that the *V. dubia* invasion could initiate a grass-fire cycle and state-shifts in historically fuel-limited forest scablands. Given that these areas were historically resistant to invasion, *V. dubia* is expanding overall invasion impacts to new ecosystems throughout the Inland Northwest, applying additional pressure on already limited fire and weed management resources. While primarily invading non-forested areas, our findings demonstrate the potential for the invasion to increase fire spread across landscapes where open areas and forests are intermixed and fire intensity in dry conifer forests, ecosystems thought to be resistant to annual grass invasion impacts. High severity fire and canopy loss could promote invasion into previously forested areas, potentially hindering post-fire forest recovery and facilitating type-conversions to annual grasslands. Overall, this work provides valuable insights into the drivers and impacts of the *V. dubia* invasion and contributes to the development of a

comprehensive invasion framework with critical implications for management practices aimed at promoting resistant and resilient landscapes.

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## APPENDICES

## Appendix A Supplementary material for Chapter 2

**Table A.1** Complete species list. \* Indicates species included in the NMS ordination after species that occurred in fewer than 5% of plots were removed to reduce noise and strengthen the relationship between community composition and environmental variables.

Latin Name	Common Name	Family	Oregon Status	Duration	Life Form
<i>Abies grandis</i>	grand fir	Pinaceae	Native	Perennial	Tree
* <i>Achillea millefolium</i>	common yarrow	Asteraceae	Native	Perennial	Forb
* <i>Achnatherum occidentale</i>	western needlegrass	Poaceae	Native	Perennial	Graminoid
* <i>Achnatherum thurberianum</i>	Thurber's needlegrass	Poaceae	Native	Perennial	Graminoid
* <i>Agoseris glauca</i>	pale agoseris	Asteraceae	Native	Perennial	Forb
* <i>Agoseris grandiflora</i>	bigflower agoseris	Asteraceae	Native	Perennial	Forb
* <i>Agoseris heterophylla</i>	annual agoseris	Asteraceae	Native	Annual	Forb
<i>Agropyron cristatum</i>	crested wheatgrass	Poaceae	Invasive	Perennial	Graminoid
<i>Agropyron intermedium</i>	intermediate wheatgrass	Poaceae	Invasive	Perennial	Graminoid
* <i>Allium acuminatum</i>	tapertip onion	Liliaceae	Native	Perennial	Forb
<i>Allium parvum</i>	small onion	Liliaceae	Native	Perennial	Forb
* <i>Allium tolmiei</i>	Tolmie's onion	Liliaceae	Native	Perennial	Forb
* <i>Alyssum alyssoides</i>	pale madwort	Brassicaceae	Invasive	Annual	Forb
<i>Amelanchier alnifolia</i>	Saskatoon serviceberry	Rosaceae	Native	Perennial	Shrub
<i>Amsinckia menziesii</i>	Menzies' fiddleneck	Boraginaceae	Native	Annual	Forb
* <i>Antennaria dimorpha</i>	low pussytoes	Asteraceae	Native	Perennial	Forb
<i>Antennaria flagellaris</i>	whip pussytoes	Asteraceae	Native	Perennial	Forb
* <i>Antennaria luzuloides</i>	rush pussytoes	Asteraceae	Native	Perennial	Forb
* <i>Antennaria microphylla</i>	littleleaf pussytoes	Asteraceae	Native	Perennial	Forb
<i>Antennaria rosea</i>	rosy pussytoes	Asteraceae	Native	Perennial	Forb
* <i>Apera interrupta</i>	dense silkybent	Poaceae	Invasive	Annual	Graminoid
* <i>Apocynum androsaemifolium</i>	spreading dogbane	Apocynaceae	Native	Perennial	Forb
<i>Arabis holboellii</i>	Holboell's rockcress	Brassicaceae	Native	Perennial	Forb
<i>Arenaria aculeata</i>	prickly sandwort	Caryophyllaceae	Native	Perennial	Forb
<i>Arenaria capillaris</i>	slender mountain sandwort	Caryophyllaceae	Native	Perennial	Forb
<i>Arenaria serpyllifolia</i>	thymeleaf sandwort	Caryophyllaceae	Invasive	Annual	Forb
* <i>Arnica cordifolia</i>	heartleaf arnica	Asteraceae	Native	Perennial	Forb
* <i>Arnica sororia</i>	twin arnica	Asteraceae	Native	Perennial	Forb
<i>Arrhenatherum elatius</i>	tall oatgrass	Poaceae	Invasive	Perennial	Graminoid
<i>Artemisia rigida</i>	scabland sagebrush	Asteraceae	Native	Perennial	Shrub
* <i>Artemisia arbuscula</i>	little sagebrush	Asteraceae	Native	Perennial	Shrub
* <i>Artemisia tridentata</i>	big sagebrush	Asteraceae	Native	Perennial	Shrub
<i>Astragalus conjunctus</i>	Idaho milkvetch	Fabaceae	Native	Perennial	Forb
* <i>Astragalus filipes</i>	basalt milkvetch	Fabaceae	Native	Perennial	Forb

<i>Astragalus misellus</i> var. <i>misellus</i>	pauper milkvetch	Fabaceae	Native	Perennial	Forb
<i>Astragalus purshii</i>	woollypod milkvetch	Fabaceae	Native	Perennial	Forb
<i>Athysanus pusillus</i>	common sandweed	Brassicaceae	Native	Annual	Forb
<i>Balsamorhiza careyana</i>	Carey's balsamroot	Asteraceae	Native	Perennial	Forb
* <i>Balsamorhiza sagittata</i>	arrowleaf balsamroot	Asteraceae	Native	Perennial	Forb
* <i>Balsamorhiza serrata</i>	serrate balsamroot	Asteraceae	Native	Perennial	Forb
* <i>Blepharipappus scaber</i>	rough eyelashweed	Asteraceae	Native	Annual	Forb
* <i>Bromus briziformis</i>	rattlesnake brome	Poaceae	Invasive	Annual	Graminoid
* <i>Bromus carinatus</i>	California brome	Poaceae	Native	Annual	Graminoid
<i>Bromus commutatus</i>	bald brome	Poaceae	Invasive	Annual	Graminoid
<i>Bromus hordeaceus</i>	soft brome	Poaceae	Invasive	Annual	Graminoid
<i>Bromus inermis</i>	smooth brome	Poaceae	Native	Perennial	Graminoid
<i>Bromus japonicus</i>	field brome	Poaceae	Invasive	Annual	Graminoid
<i>Bromus squarrosus</i>	corn brome	Poaceae	Invasive	Annual	Graminoid
* <i>Bromus tectorum</i>	cheatgrass	Poaceae	Invasive	Annual	Graminoid
* <i>Calamagrostis rubescens</i>	pinegrass	Poaceae	Native	Perennial	Graminoid
* <i>Calochortus eurycarpus</i>	white mariposa lily	Liliaceae	Native	Perennial	Forb
* <i>Calochortus macrocarpus</i>	sagebrush mariposa lily	Liliaceae	Native	Perennial	Forb
<i>Camassia quamash</i>	small camas	Liliaceae	Native	Perennial	Forb
<i>Carex filifolia</i>	threadleaf sedge	Cyperaceae	Native	Perennial	Graminoid
* <i>Carex geyeri</i>	Geyer's sedge	Cyperaceae	Native	Perennial	Graminoid
<i>Carex subfusca</i>	brown sedge	Cyperaceae	Native	Perennial	Graminoid
<i>Castilleja applegatei</i>	wavyleaf Indian paintbrush	Scrophulariaceae	Native	Perennial	Forb
* <i>Castilleja miniata</i>	giant red Indian paintbrush	Scrophulariaceae	Native	Perennial	Forb
<i>Castilleja oresbia</i>	pale Wallowa Indian paintbrush	Scrophulariaceae	Native	Perennial	Forb
* <i>Castilleja tenuis</i>	hairy Indian paintbrush	Scrophulariaceae	Native	Annual	Forb
* <i>Ceanothus velutinus</i>	snowbrush ceanothus	Rhamnaceae	Native	Perennial	Shrub
<i>Ceratocephala testiculata</i>	curveseed butterwort	Ranunculaceae	Invasive	Annual	Forb
* <i>Cercocarpus ledifolius</i>	curl-leaf mountain mahogany	Rosaceae	Native	Perennial	Tree
<i>Chaenactis douglasii</i>	Douglas' dustymaiden	Asteraceae	Native	Perennial	Forb
* <i>Chamaesyce glyptosperma</i>	ribseed sandmat	Euphorbiaceae	Native	Annual	Forb
<i>Chrysothamnus viscidiflorus</i>	yellow rabbitbrush	Asteraceae	Native	Perennial	Shrub
<i>Cirsium vulgare</i>	bull thistle	Asteraceae	Invasive	Perennial	Forb
* <i>Clarkia pulchella</i>	pinkfairies	Onagraceae	Native	Annual	Forb
<i>Clarkia rhomboidea</i>	diamond clarkia	Onagraceae	Native	Annual	Forb
<i>Claytonia linearis</i>	narrowleaf minerslettuce	Portulacaceae	Native	Annual	Forb
* <i>Claytonia perfoliata</i>	miner's lettuce	Portulacaceae	Native	Annual	Forb
* <i>Collinsia parviflora</i>	maiden blue eyed Mary	Scrophulariaceae	Native	Annual	Forb
* <i>Collomia grandiflora</i>	grand collomia	Polemoniaceae	Native	Annual	Forb
<i>Collomia linearis</i>	tiny trumpet	Polemoniaceae	Native	Annual	Forb

<i>Cordylanthus ramosus</i>	bushy bird's beak	Scrophulariaceae	Native	Annual	Forb
<i>Crepis acuminata</i>	tapertip hawksbeard	Asteraceae	Native	Perennial	Forb
* <i>Crepis atriobarba</i>	slender hawksbeard	Asteraceae	Native	Perennial	Forb
* <i>Crepis occidentalis</i>	largeflower hawksbeard	Asteraceae	Native	Annual	Forb
* <i>Crocidium multicaule</i>	common spring-gold	Asteraceae	Native	Annual	Forb
<i>Cryptantha flaccida</i>	weakstem cryptantha	Boraginaceae	Native	Annual	Forb
<i>Cystopteris fragilis</i>	brittle bladderfern	Dryopteridaceae	Native	Perennial	Forb
<i>Dalea ornata</i>	Blue Mountain prairie clover	Fabaceae	Native	Perennial	Forb
* <i>Danthonia unispicata</i>	onespike danthonia	Poaceae	Native	Perennial	Graminoid
<i>Delphinium nuttallianum</i>	twolobe larkspur	Ranunculaceae	Native	Perennial	Forb
* <i>Deschampsia danthonioides</i>	annual hairgrass	Poaceae	Native	Annual	Graminoid
<i>Descurainia pinnata</i>	western tansymustard	Brassicaceae	Native	Annual	Forb
<i>Dianthus armeria</i>	Deptford pink	Caryophyllaceae	Invasive	Annual	Forb
<i>Diplacus nanus</i>	dwarf purple monkeyflower	Scrophulariaceae	Native	Annual	Forb
* <i>Draba verna</i>	spring draba	Brassicaceae	Invasive	Annual	Forb
<i>Dryocallis glandulosa</i>	sticky cinquefoil	Rosaceae	Native	Perennial	Forb
<i>Eleocharis palustris</i>	common spikerush	Cyperaceae	Native	Perennial	Graminoid
* <i>Elymus elymoides</i>	squirreltail	Poaceae	Native	Perennial	Graminoid
<i>Elymus glaucus</i>	blue wildrye	Poaceae	Native	Perennial	Graminoid
<i>Epilobium angustifolium</i>	fireweed	Onagraceae	Native	Perennial	Forb
* <i>Epilobium brachycarpum</i>	tall annual willowherb	Onagraceae	Native	Annual	Forb
<i>Epilobium ciliatum</i>	fringed willowherb	Onagraceae	Native	Perennial	Forb
* <i>Ericameria nauseosa</i>	rubber rabbitbrush	Asteraceae	Native	Perennial	Shrub
<i>Erigeron aphanactis</i>	rayless shaggy fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron bloomeri</i>	scabland fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron chrysopsidis</i>	dwarf yellow fleabane	Asteraceae	Native	Perennial	Forb
* <i>Erigeron corymbosus</i>	longleaf fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron filifolius</i>	threadleaf fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron inornatus</i>	California rayless fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron linearis</i>	desert yellow fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron poliospermus</i>	purple cushion fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron pumilus</i>	shaggy fleabane	Asteraceae	Native	Perennial	Forb
<i>Erigeron speciosus</i>	aspen fleabane	Asteraceae	Native	Perennial	Forb
<i>Eriogonum compositum</i>	arrowleaf buckwheat	Polygonaceae	Native	Perennial	Forb
<i>Eriogonum elatum</i>	tall woolly buckwheat	Polygonaceae	Native	Perennial	Forb
* <i>Eriogonum heracleoides</i>	parsnipflower buckwheat	Polygonaceae	Native	Perennial	Forb
<i>Eriogonum nudum</i>	naked buckwheat	Polygonaceae	Native	Perennial	Forb
<i>Eriogonum sphaerocephalum</i>	rock buckwheat	Polygonaceae	Native	Perennial	Forb
<i>Eriogonum umbellatum</i>	sulphur-flower buckwheat	Polygonaceae	Native	Perennial	Forb
<i>Eriogonum vimineum</i>	wickerstem buckwheat	Polygonaceae	Native	Annual	Forb
<i>Eriophyllum lanatum</i>	common woolly sunflower	Asteraceae	Native	Annual	Forb

<i>*Erodium cicutarium</i>	redstem stork's bill	Geraniaceae	Invasive	Annual	Forb
<i>*Festuca idahoensis</i>	Idaho fescue	Poaceae	Native	Perennial	Graminoid
<i>Fragaria vesca</i>	woodland strawberry	Rosaceae	Native	Perennial	Forb
<i>*Fragaria virginiana</i>	Virginia strawberry	Rosaceae	Native	Perennial	Forb
<i>*Fritillaria pudica</i>	yellow fritillary	Liliaceae	Native	Perennial	Forb
<i>*Galium aparine</i>	stickywilly	Rubiaceae	Native	Annual	Forb
<i>Galium boreale</i>	northern bedstraw	Rubiaceae	Native	Perennial	Forb
<i>Gayophytum diffusum</i>	spreading groundsmoke	Onagraceae	Native	Annual	Forb
<i>Gayophytum ramosissimum</i>	pinyon groundsmoke	Onagraceae	Native	Annual	Forb
<i>Gayophytum sp</i>	groundsmoke	Onagraceae	Native	Annual	Forb
<i>Geranium viscosissimum</i>	sticky purple geranium	Geraniaceae	Native	Annual	Forb
<i>*Geum triflorum</i>	old man's whiskers	Rosaceae	Native	Perennial	Forb
<i>Grindelia nana</i>	Idaho gumweed	Asteraceae	Native	Perennial	Forb
<i>*Hackelia micrantha</i>	Jessica sticktight	Boraginaceae	Native	Perennial	Forb
<i>Helianthella uniflora</i>	oneflower helianthella	Asteraceae	Native	Perennial	Forb
<i>*Hemizonella minima</i>	opposite-leaved tarweed	Asteraceae	Native	Annual	Forb
<i>*Hesperolinon micranthum</i>	smallflower dwarf-flax	Linaceae	Native	Annual	Forb
<i>Hesperostipa comata</i>	needle and thread	Poaceae	Native	Perennial	Graminoid
<i>Hieracium albertinum</i>	Scouler's woollyweed	Asteraceae	Native	Perennial	Forb
<i>Hieracium albiflorum</i>	white hawkweed	Asteraceae	Native	Perennial	Forb
<i>*Holosteum umbellatum</i>	jagged chickweed	Caryophyllaceae	Invasive	Annual	Forb
<i>*Idahoa scapigera</i>	oldstem idahoa	Brassicaceae	Native	Annual	Forb
<i>Iliamna rivularis</i>	streambank wild hollyhock	Malvaceae	Native	Perennial	Forb
<i>Ipomopsis aggregata</i>	scarlet gilia	Polemoniaceae	Native	Perennial	Forb
<i>Juncus confusus</i>	Colorado rush	Juncaceae	Native	Perennial	Graminoid
<i>*Juniperus occidentalis</i>	western juniper	Cupressaceae	Native	Perennial	Tree
<i>*Koeleria macrantha</i>	prairie Junegrass	Poaceae	Native	Perennial	Graminoid
<i>*Lactuca serriola</i>	prickly lettuce	Asteraceae	Invasive	Annual	Forb
<i>*Lagophylla ramosissima</i>	branched lagophylla	Asteraceae	Native	Annual	Forb
<i>Larix occidentalis</i>	western larch	Pinaceae	Native	Perennial	Tree
<i>Lepidium perfoliatum</i>	clasping pepperweed	Brassicaceae	Invasive	Annual	Forb
<i>Leptosiphon liniflorus</i>	narrowflower flaxflower	Polemoniaceae	Native	Annual	Forb
<i>*Lewisia rediviva</i>	bitter root	Portulacaceae	Native	Perennial	Forb
<i>Linanthus harknessii</i>	Harkness' flaxflower	Polemoniaceae	Native	Annual	Forb
<i>Linum lewisii</i>	Lewis flax	Linaceae	Native	Perennial	Forb
<i>*Lithophragma parviflorum</i>	smallflower woodland-star	Saxifragaceae	Native	Perennial	Forb
<i>*Lithophragma tenellum</i>	slender woodland-star	Saxifragaceae	Native	Perennial	Forb
<i>*Lithospermum ruderales</i>	western stoneseed	Boraginaceae	Native	Perennial	Forb
<i>Lomatium cous</i>	cous biscuitroot	Apiaceae	Native	Perennial	Forb
<i>Lomatium grayi</i>	Gray's biscuitroot	Apiaceae	Native	Perennial	Forb
<i>Lomatium leptocarpum</i>	Wasatch desertparsley	Apiaceae	Native	Perennial	Forb



<i>*Lomatium macrocarpum</i>	bigseed biscuitroot	Apiaceae	Native	Perennial	Forb
<i>*Lomatium nudicaule</i>	barestem biscuitroot	Apiaceae	Native	Perennial	Forb
<i>*Lomatium triternatum</i>	nineleaf biscuitroot	Apiaceae	Native	Perennial	Forb
<i>Lomatium vaginatum</i>	broadsheath desertparsley	Apiaceae	Native	Perennial	Forb
<i>Lotus denticulatus</i>	riverbar bird's-foot trefoil	Fabaceae	Native	Annual	Forb
<i>*Lupinus caudatus</i>	tailcup lupine	Fabaceae	Native	Perennial	Forb
<i>Lupinus laxiflorus</i>	longspur lupine	Fabaceae	Native	Perennial	Forb
<i>Lupinus leucophyllus</i>	velvet lupine	Fabaceae	Native	Perennial	Forb
<i>*Madia exigua</i>	small tarweed	Asteraceae	Native	Annual	Forb
<i>Madia glomerata</i>	mountain tarweed	Asteraceae	Native	Annual	Forb
<i>*Madia gracilis</i>	grassy tarweed	Asteraceae	Native	Annual	Forb
<i>*Mahonia repens</i>	creeping barberry	Berberidaceae	Native	Perennial	Forb
<i>Melica spectabilis</i>	purple oniongrass	Poaceae	Native	Perennial	Graminoid
<i>Mentzelia dispersa</i>	bushy blazingstar	Loasaceae	Native	Annual	Forb
<i>*Microsteris gracilis</i>	slender phlox	Polemoniaceae	Native	Annual	Forb
<i>*Myosotis stricta</i>	strict forget-me-not	Boraginaceae	Invasive	Annual	Forb
<i>*Navarretia divaricata</i>	divaricate navarretia	Polemoniaceae	Native	Annual	Forb
<i>Navarretia intertexta</i>	needleleaf navarretia	Polemoniaceae	Native	Annual	Forb
<i>*Nemophila parviflora</i>	smallflower nemophila	Hydrophyllaceae	Native	Annual	Forb
<i>Noccaea montana</i>	Fendler's pennycress	Brassicaceae	Native	Perennial	Forb
<i>*Nothocalais troximoides</i>	sagebrush false dandelion	Asteraceae	Native	Perennial	Forb
<i>Orobanche uniflora</i>	oneflowered broomrape	Orobanchaceae	Native	Annual	Forb
<i>Orthocarpus tenuifolius</i>	thinleaved owl's-clover	Scrophulariaceae	Native	Annual	Forb
<i>Osmorhiza occidentalis</i>	western sweetroot	Apiaceae	Native	Perennial	Forb
<i>Paeonia brownii</i>	Brown's peony	Paeoniaceae	Native	Perennial	Forb
<i>Penstemon attenuatus</i>	sulphur penstemon	Scrophulariaceae	Native	Perennial	Forb
<i>Penstemon deustus</i>	scabland penstemon	Scrophulariaceae	Native	Perennial	Forb
<i>Penstemon fruticosus</i>	bush penstemon	Scrophulariaceae	Native	Perennial	Forb
<i>Penstemon gairdneri</i> var. <i>gairdneri</i>	Gairdner's beardtongue	Scrophulariaceae	Native	Perennial	Forb
<i>Penstemon laetus</i>	mountain blue penstemon	Scrophulariaceae	Native	Perennial	Forb
<i>Perideridia gairdneri</i>	Gardner's yampah	Apiaceae	Native	Perennial	Forb
<i>Phacelia hastata</i>	silverleaf phacelia	Hydrophyllaceae	Native	Perennial	Forb
<i>*Phacelia heterophylla</i>	varileaf phacelia	Hydrophyllaceae	Native	Perennial	Forb
<i>Phacelia linearis</i>	threadleaf phacelia	Hydrophyllaceae	Native	Annual	Forb
<i>Phleum pratense</i>	timothy	Poaceae	Invasive	Perennial	Graminoid
<i>Phlox aculeata</i>	sagebrush phlox	Polemoniaceae	Native	Perennial	Forb
<i>*Phlox hoodii</i>	spiny phlox	Polemoniaceae	Native	Perennial	Forb
<i>Phlox sp</i>	phlox	Polemoniaceae	Native	Perennial	Forb
<i>*Phoenicaulis cheiranthoides</i>	wallflower phoenicaulis	Brassicaceae	Native	Perennial	Forb
<i>*Pinus ponderosa</i>	ponderosa pine	Pinaceae	Native	Perennial	Tree
<i>Plagiobothrys tenellus</i>	Pacific popcornflower	Boraginaceae	Native	Annual	Forb

<i>*Plectritis macrocera</i>	longhorn plectritis	Valerianaceae	Native	Annual	Forb
<i>*Poa bulbosa</i>	bulbous bluegrass	Poaceae	Invasive	Perennial	Graminoid
<i>*Poa pratensis</i>	Kentucky bluegrass	Poaceae	Invasive	Perennial	Graminoid
<i>*Poa secunda</i>	Sandberg bluegrass	Poaceae	Native	Perennial	Graminoid
<i>*Polygonum douglasii</i>	Douglas' knotweed	Polygonaceae	Native	Annual	Forb
<i>*Polygonum polygaloides</i>	milkwort knotweed	Polygonaceae	Native	Annual	Forb
<i>*Potentilla gracilis</i>	slender cinquefoil	Rosaceae	Native	Perennial	Forb
<i>Poteridium occidentale</i>	prairie burnet	Rosaceae	Native	Annual	Forb
<i>Prunus emarginata</i>	bitter cherry	Rosaceae	Native	Perennial	Shrub
<i>*Pseudoroegneria spicata</i>	bluebunch wheatgrass	Poaceae	Native	Perennial	Graminoid
<i>*Pseudotsuga menziesii</i>	Douglas-fir	Pinaceae	Native	Perennial	Tree
<i>*Purshia tridentata</i>	antelope bitterbrush	Rosaceae	Native	Perennial	Shrub
<i>*Pyrrocoma carthamoides</i>	largeflower goldenweed	Asteraceae	Native	Perennial	Forb
<i>Ranunculus uncinatus</i>	woodland buttercup	Ranunculaceae	Native	Annual	Forb
<i>*Ribes cereum</i>	wax currant	Grossulariaceae	Native	Perennial	Shrub
<i>Rigiopappus leptocladus</i>	wireweed	Asteraceae	Native	Annual	Forb
<i>*Rosa gymnocarpa</i>	dwarf rose	Rosaceae	Native	Perennial	Shrub
<i>Rumex acetosella</i>	common sheep sorrel	Polygonaceae	Invasive	Perennial	Forb
<i>Salix sp.</i>	willow	Salicaceae	Native	Perennial	Shrub
<i>Sambucus racemosa</i>	red elderberry	Caprifoliaceae	Native	Perennial	Shrub
<i>Saxifraga integrifolia</i>	wholeleaf saxifrage	Saxifragaceae	Native	Perennial	Forb
<i>Scutellaria antirrhinoides</i>	nose skullcap	Lamiaceae	Native	Perennial	Forb
<i>*Sedum stenopetalum</i>	wormleaf stonecrop	Crassulaceae	Native	Perennial	Forb
<i>*Senecio integerrimus</i>	lambs tongue ragwort	Asteraceae	Native	Perennial	Forb
<i>*Sidalcea oregana</i>	Oregon checkerbloom	Malvaceae	Native	Perennial	Forb
<i>Silene douglasii</i>	Douglas's catchfly	Caryophyllaceae	Native	Perennial	Forb
<i>Silene menziesii</i>	Menzies' campion	Caryophyllaceae	Native	Perennial	Forb
<i>Silene oregana</i>	Oregon silene	Caryophyllaceae	Native	Perennial	Forb
<i>Silene scaposa</i>	Blue Mountain catchfly	Caryophyllaceae	Native	Perennial	Forb
<i>*Sisymbrium altissimum</i>	tall tumbled mustard	Brassicaceae	Invasive	Annual	Forb
<i>*Sisyrinchium idahoense</i>	Idaho blue-eyed grass	Iridaceae	Native	Perennial	Forb
<i>*Solidago missouriensis</i>	Missouri goldenrod	Asteraceae	Native	Perennial	Forb
<i>Stellaria longipes</i>	longstalk starwort	Caryophyllaceae	Native	Perennial	Forb
<i>Stenotus lanuginosus</i>	woolly mock goldenweed	Asteraceae	Native	Perennial	Forb
<i>*Symphoricarpos albus</i>	common snowberry	Caprifoliaceae	Native	Perennial	Shrub
<i>Symphoricarpos oreophilus</i>	mountain snowberry	Caprifoliaceae	Native	Perennial	Shrub
<i>Symphyotrichum campestre</i>	western meadow aster	Asteraceae	Native	Perennial	Forb
<i>Symphyotrichum spathulatum</i>	western mountain aster	Asteraceae	Native	Perennial	Forb
<i>*Taeniatherum caput-medusae</i>	medusahead	Poaceae	Invasive	Annual	Graminoid
<i>Taraxacum officinale</i>	common dandelion	Asteraceae	Invasive	Perennial	Forb
<i>Tetradymia canescens</i>	spineless horsebrush	Asteraceae	Native	Perennial	Shrub

<i>Thalictrum occidentale</i>	western meadow-rue	Ranunculaceae	Native	Perennial	Forb
<i>Thysanocarpus curvipes</i>	sand fringe-pod	Brassicaceae	Native	Annual	Forb
* <i>Tragopogon dubius</i>	yellow salsify	Asteraceae	Invasive	Annual	Forb
<i>Trifolium cyathiferum</i>	cup clover	Fabaceae	Native	Annual	Forb
* <i>Trifolium macrocephalum</i>	largehead clover	Fabaceae	Native	Perennial	Forb
<i>Trisetum spicatum</i>	spike trisetum	Poaceae	Native	Perennial	Graminoid
* <i>Triteleia grandiflora</i>	largeflower triteleia	Liliaceae	Native	Perennial	Forb
<i>Triteleia hyacinthina</i>	white brodiaea	Liliaceae	Native	Perennial	Forb
* <i>Ventenata dubia</i>	North Africa grass	Poaceae	Invasive	Annual	Graminoid
<i>Verbascum thapsus</i>	common mullein	Scrophulariaceae	Invasive	Perennial	Forb
<i>Veronica serpyllifolia</i>	thymeleaf speedwell	Scrophulariaceae	Native	Perennial	Forb
* <i>Vulpia microstachys</i>	small fescue	Poaceae	Native	Annual	Graminoid
<i>Vulpia myuros</i>	annual fescue	Poaceae	Invasive	Annual	Graminoid
* <i>Wyethia amplexicaulis</i>	mule-ears	Asteraceae	Native	Perennial	Forb
<i>Zigadenus paniculatus</i>	foothill deathcamas	Liliaceae	Native	Perennial	Forb
<i>Zigadenus venenosus</i>	meadow deathcamas	Liliaceae	Native	Perennial	Forb

**Table A.2** Descriptions of all environmental variables included in NMS ordinations. We identified correlated predictor variables and removed all but the variable with the highest  $R^2$  values for each axis from the figure to improve readability and interpretability of the ordinations.

\*Indicate variables that were removed from the visualization of the NMS ordination.

Attribute	Description	Scale of Measurement	Source of Data	Min	Max	Cor. to NMS Axis 1		Cor. to NMS Axis 2		Cor. to NMS Axis 3	
						r	tau	r	tau	r	tau
<b>Climate</b>											
<b>Heat load</b>	Heat load - calculated with McCune's (2007) heatload metric	plot center	McCune 2007	-0.6	0.8	0.1	0.0	0.0	0.0	0.0	0.0
<b>PDIR</b>	Potential direct incident radiation - calculated with McCune's (2007) PDIR metric	plot center	McCune 2007	-0.6	1.2	0.1	0.0	-0.1	-0.1	-0.1	0.0
<b>Precip 2018</b>	precipitation Jan. - Jun. 2018 (mm)	plot center (800m)	PRISM - 800m	114.1	365.9	-0.3	-0.2	-0.3	-0.1	-0.3	-0.3
<b>PRISM 30</b>	precipitation 30year normal (mm)	plot center (800m)	PRISM - 800m	270.6	724.1	-0.3	-0.2	-0.3	-0.1	-0.4	-0.3
<b>Tmax</b>	30-yr normal max temperature (deg C)	plot center	PRISM - 800m	11.1	16.9	-0.2	-0.1	-0.6	-0.4	-0.4	-0.3
<b>Tmean*</b>	30-yr normal mean temperature (deg C)	plot center	PRISM - 800m	5.6	9.8	-0.3	-0.1	-0.5	-0.3	-0.4	-0.3
<b>Disturbance</b>											
<b>Disturbance</b>	Disturbance by grazing, burn, anthropogenic disturbance: 0 = undisturbed (0% vegetation/ soil disturbed by fire), 1 = low (<10%), 2 = moderate (10-50%), 3 = high (>50%)	plot	Field measurement	0.0	3.0	-0.1	-0.1	0.3	0.2	-0.5	-0.4
<b>Grazed</b>	evidence of grazing present in plot (1 = grazing evidence; 0 = no grazing evidence)	quadrat	Field measurement	0.0	1.0	0.0	0.0	0.2	0.2	0.0	0.0
<b>Nearest Road</b>	Nearest road to plot (m)	plot center	ODOT spatial layer	7.8	1749.0	0.2	0.2	-0.1	-0.2	-0.3	-0.2
<b>Fire</b>											
<b>Burn evidence*</b>	% of quadrats in a plot exhibiting some evidence of burning	quadrat	Field measurement	0.0	100.0	0.0	0.0	0.2	0.1	-0.4	-0.3
<b>Fire severity</b>	Burn severity estimate, 0 = unburned (0% vegetation/ soil disturbed by fire), 1 = low (<10%), 2 = moderate (10-50%), 3 = high (>50%)	plot	Field measurement	0.0	3.0	0.0	0.0	0.0	0.0	-0.4	-0.3
<b>Burned</b>	Any evidence of burning inside the plot results in the plot being labeled "Burned = 1" vs. "Unburned = 0"	plot	Field measurement	0.0	1.0	0.0	0.0	0.0	0.0	-0.3	-0.3
<b>DBNR</b>	Burn severity calculated with DNBR from Google earth engine	plot center (30m)	30-meter Landsat TM+	-128.8	548.4	0.1	0.1	0.2	0.1	-0.2	-0.1

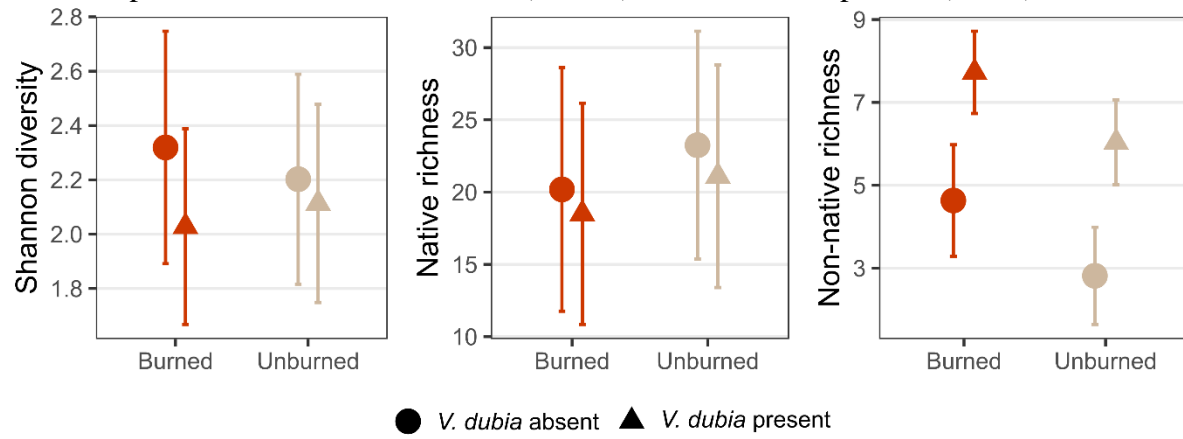
			satellite imagery								
Geology											
Andesite	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	0.0	0.0	0.3	0.2	-0.2	-0.2
Argillite	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	-0.4	-0.3	0.2	0.2	0.2	0.2
Basalt	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	0.5	0.4	0.1	0.1	0.1	0.1
Mixed clastic/volcanic	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	0.0	0.0	0.0	0.0	-0.1	-0.1
Mudstone	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	-0.2	-0.2	-0.2	-0.2	0.1	0.1
Peridotite	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	0.1	0.0	-0.1	-0.1	-0.2	-0.1
Rhyolite	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	0.1	0.1	0.0	0.0	0.1	0.1
Sandstone	geologic substrate	plot center	Ludington et al. 2015; USGS Geology of OR spatial layer	0.0	1.0	-0.4	-0.3	-0.4	-0.3	-0.2	-0.2
Ground cover											
Bare ground	bare ground cover (%) averaged to plot (loose mineral soil)	quadrat	Field measurement	0.2	64.4	-0.6	-0.4	-0.1	0.0	0.0	0.0
Crust	biological and/or chemical crust cover (i.e. not loose mineral soil/ bare ground) averaged to plot (%)	quadrat	Field measurement	0.0	46.4	-0.1	0.1	-0.4	-0.2	0.3	0.2

<b>Gravel</b>	rock (<5cm) cover averaged to plot (%)	quadrat	Field measurement	0.0	67.2	0.1	0.1	-0.3	-0.3	0.4	0.2
<b>Litter cover</b>	herbaceous litter cover and duff cover averaged to plot (%)	quadrat	Field measurement	3.9	83.7	0.0	0.0	0.7	0.5	-0.4	-0.3
<b>Litter depth*</b>	average depth of litter/duff (mm)	quadrat	Field measurement	0.0	22.4	-0.1	-0.1	0.6	0.5	-0.2	-0.2
<b>Rock/cobble</b>	rock (>5cm) cover averaged to plot (%)	quadrat	Field measurement	0.0	46.2	0.4	0.3	-0.4	-0.3	0.1	0.1
<b>Short moss</b>	short moss (<1cm) cover averaged to plot (%)	quadrat	Field measurement	0.0	35.3	0.2	0.2	-0.1	-0.1	0.0	0.1
<b>Tall moss</b>	tall moss (>1cm) cover averaged to plot (%)	quadrat	Field measurement	0.0	43.1	0.4	0.3	-0.3	-0.1	0.1	0.2
<b>Moss</b>	tall moss cover + short moss cover (%)	Quadrat	Field measurement	0.0	45.6	0.4	0.3	-0.3	-0.2	0.1	0.1
<b>Woody litter*</b>	% woody litter cover averaged to plot	quadrat	Field measurement	0.0	29.7	-0.2	-0.2	0.6	0.4	-0.2	-0.1
<b>Soil</b>											
<b>LOI (0-10cm)*</b>	Loss on ignition for top 10 cm of soil averaged to plot	transect	Field measurement; Nelson & Sommers, 1996	0.0	0.3	-0.2	-0.1	0.6	0.5	0.0	0.0
<b>LOI (10-20cm)</b>	Loss on ignition for 10-20 cm of soil averaged to plot	transect	Field measurement; Nelson & Sommers, 1996	0.0	0.2	0.0	-0.1	0.6	0.5	0.0	0.0
<b>P (0-10cm)</b>	Phosphorous for top 10 cm of soil averaged to plot (N=58). Missing values were input as averages for the fire perimeter for NMS.	transect	Field measurement; Olsen & Sommers, 1982	0.4	73.9	-0.5	-0.3	0.1	0.0	0.1	0.1
<b>P (10-20cm)*</b>	Phosphorous for 10-20 cm of soil averaged to plot (N=58). Missing values were input as averages for the fire for NMS.	transect	Field measurement; Olsen & Sommers, 1982	0.4	24.6	-0.5	-0.3	0.1	0.1	0.0	0.0
<b>pH (0-10cm)</b>	pH of top 10cm of soil averaged to plot	transect	Field measurement; Thomas, 1996	6.2	8.5	0.2	0.2	-0.5	-0.4	0.2	0.1
<b>pH (10-20cm)*</b>	pH of soil sample 10 - 20cm deep averaged to plot	transect	Field measurement; Thomas, 1996	6.5	8.4	0.4	0.2	-0.4	-0.3	0.0	0.0
<b>Soil depth</b>	soil depth of 3 samples averaged to plot (cm)	transect	Field measurement	1.7	>30	-0.3	-0.2	0.3	0.2	-0.1	-0.1
<b>Sand</b>	soil texture class for top 10cm of soil converted to mean % sand	transect	Hand texture;	10.0	92.0	-0.20	-0.11	0.10	0.04	-0.02	-0.02

			Thien, 1978								
<b>Silt</b>	soil texture class for top 10cm of soil converted to mean % silt	transect	Hand texture; Thien, 1978	5.0	85.0	0.04	0.08	0.01	0.02	-0.07	-0.03
<b>Clay</b>	soil texture class for top 10cm of soil converted to mean % clay	transect	Hand texture; Thien, 1978	3.0	58.0	0.32	0.23	-0.20	-0.15	0.14	0.07
<b>Topographic</b>											
<b>Aspect</b>	compass direction that the slope is facing	plot	Field measurement	4.0	358.0	0.0	0.1	0.1	0.1	0.0	-0.1
<b>Slope Shape</b>	slope shape described perpendicular to elevation contour and along elevation contour: L = linear, CV = convex, CC = concave	plot center	Field measurement; USDA-NRCS 2012: Field book for describing soils	0.0	1.0						
<b>Elevation</b>	Elevation measured from DEM	plot	DEM	751.5	2053.9	0.3	0.1	0.6	0.3	0.4	0.3
<b>Slope</b>	average slope of the plot	plot	Field measurement	0.0	38.0	-0.2	-0.1	0.4	0.3	-0.1	-0.1
<b>Vegetation</b>											
<b>Canopy cover</b>	Canopy cover	plot center	GNN	0.0	45.0	0.0	-0.1	0.4	0.4	-0.2	-0.1
<b>Basal Area*</b>	Basal area - estimated by all trees in plot (standing and recently downed)	plot & transect	Field measurement	0.0	13.8	0.0	-0.1	0.6	0.5	-0.3	-0.2

**Table A.3**

Mean Shannon diversity and species richness with 95% confidence intervals in burned and unburned plots where *V. dubia* is absent (N = 33) and *V. dubia* is present (N=77).

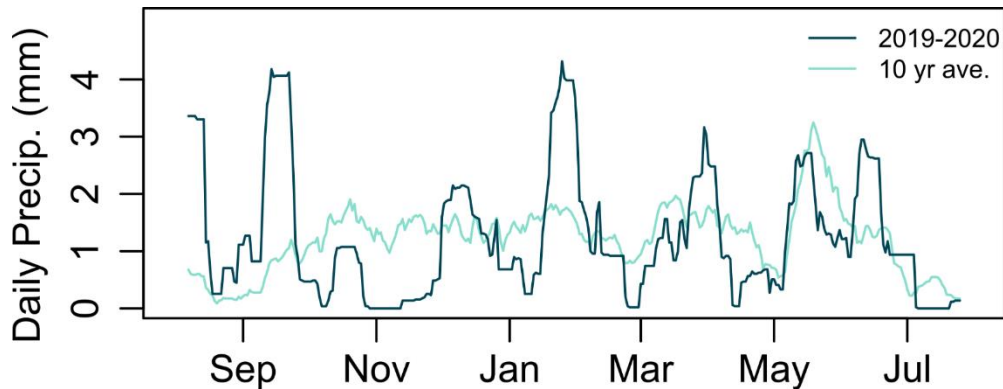




## Appendix B Supplementary material for Chapter 3

### Appendix B.1 Climate information

**Figure B.1.1:** Precipitation recorded from the Brer Rabbit remote automatic weather station (RAWS) located within the Ochoco National Forest near the sample sites (Western Regional Climate Center 2021). We compared precipitation from the sample season, August 2019 through July 2020 (just before *V. dubia* seeds were added to subplots until just after *V. dubia* biomass was harvested), and a ten year average (August 2010 through July 2020). We chose a ten year average to represent precipitation conditions from the period in which *V. dubia* was established widely throughout the National Forest. Daily precipitation values were smoothed for plotting using a moving average with a 14-day window with the package ‘stats’ (R core Team 2021).



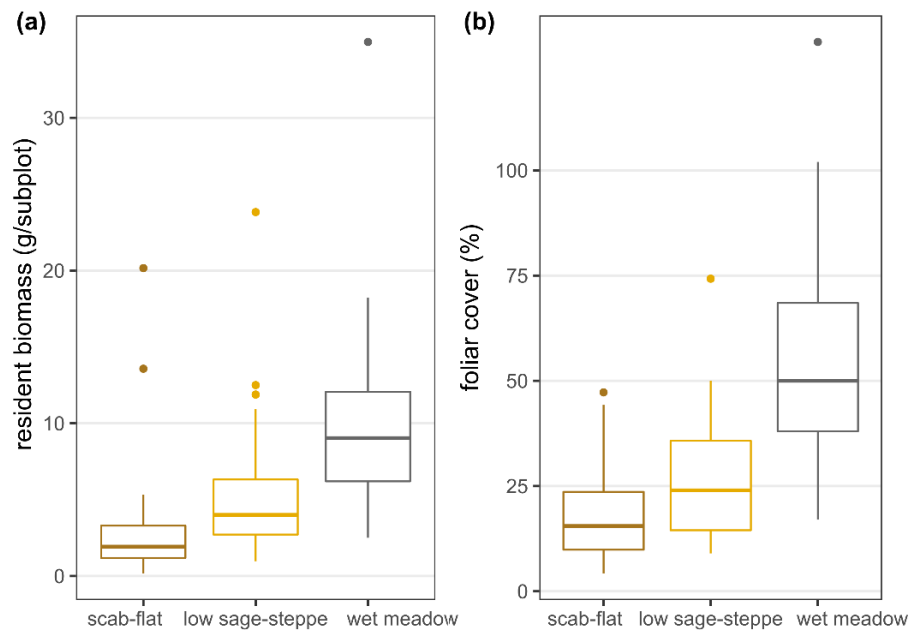
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- Western Regional Climate Center. 2021. Brer Rabbit Oregon. Retrieved from <https://raws.dri.edu/cgi-bin/rawMAIN.pl?orOBRI>.

## Appendix B.2 Testing the productivity gradient

We examined the extent to which the three vegetation types chosen represented a true vegetative productivity gradient by modeling resident biomass and foliar cover response to vegetation type. Resident biomass was modeled using a linear mixed effects model. Biomass was log transformed prior to modeling to account for it being log-normally distributed. Foliar cover was modeled using a generalized linear mixed effects model from the package glmmTMB (Brooks et al. 2017) with a ‘tweedie’ distribution and log-link to account for the high proportion of zeros present in cover data (Tweedie 1984).

Resident biomass and foliar cover increased with increasing soil depth and perceived soil moisture, based on species associations at each vegetation type (Paulson 1977). Mean biomass was 4.4 (95% CI: 2.6-7.3) times higher in wet meadows than in scab-flats and 2.1 (95% CI: 1.2-3.5) times higher than in low-sage steppe. Mean foliar cover was 3.0 (95% CI: 2.0-4.5) times higher in wet meadows than in scab-flats and 2.1 (95% CI: 1.4-3.1) times higher than in low-sage steppe. In the low sage-steppe, mean biomass and foliar cover were 2.1 (1.3-3.5) and 1.5 (1.0-2.2) times higher than in scab-flats, respectively.



**Figure 3.2.1 (a) Resident biomass and (b) total percent foliar cover (excluding *V. dubia*) per subplot by vegetation type. Foliar cover could exceed 100% if multiple species were overlapping.**

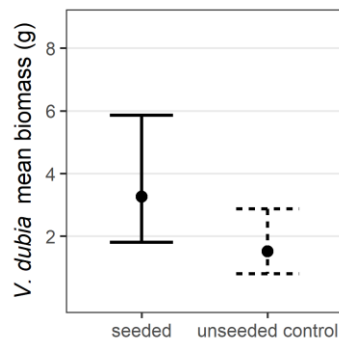
**References**

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- Tweedie, M. C. K. 1984. An index which distinguishes between some important exponential families. Statistics: Applications and New Directions. Proceedings of the Indian Statistical Institute Golden Jubilee International Conference.

### Appendix B.3 Additional details about methods

Expanding on the evaluation of “unseeded controls”: We tested for differences in *V. dubia* biomass between “seeded” and “unseeded control” subplots using linear mixed effects models including an interaction with vegetation type and random effects for block and site.

Mean *V. dubia* biomass in seeded subplots was 215% ( $p < 0.001$ ) higher than in unseeded controls (representing natural *V. dubia* regeneration after initial *V. dubia* removal). We did not find evidence that the effectiveness of the seed addition treatment was influenced by vegetation type (chi-squared for treatment-vegetation type interaction = 0.002;  $p = 0.99$ ).



**Figure B.3.1** *Ventenata dubia* biomass (g) in seeded subplots and unseeded controls

Expanding upon the nearest species dissimilarity metric calculations: When *V. dubia*’s trait value fell above or below all neighbor trait values, resulting in only one neighbor, we doubled the trait distance of that neighbor. However, in the case that *V. dubia* had the lowest trait value and the distance to the nearest neighbor was greater than *V. dubia*’s trait value, we did not double the trait distance assuming that *V. dubia* could occupy trait space between the neighbor and 0, but not below 0 (following Catford et al. 2019).

## Appendix B.4: Species list and traits

**Table B.4.1:** Species list for species included in trait analysis. Nomenclature follows USDA Plants Database, 2020.

USDA plant code	Latin name	Duration	Native status
AGHE2	<i>Agoseris heterophylla</i>	Annual	Native
ALAC4	<i>Allium acuminatum</i>	Perennial	Native
ALLIU	<i>Allium</i> sp.	Perennial	Native
ANLU2	<i>Antennaria luzuloides</i>	Perennial	Native
BRAR5	<i>Bromus arvensis</i>	Annual	Introduced
BRTE	<i>Bromus tectorum</i>	Annual	Introduced
CAQU2	<i>Camassia quamash</i>	Perennial	Native
CATE26	<i>Castilleja tenuis</i>	Annual	Native
COPA3	<i>Collinsia parviflora</i>	Annual	Native
DAUN	<i>Danthonia unispicata</i>	Perennial	Native
DEDA	<i>Deschampsia danthonioides</i>	Annual	Native
DEDI11	<i>Delphinium distichum</i>	Perennial	Native
DODEC	<i>Dodecatheon</i> sp.	Perennial	Native
ELBE	<i>Eleocharis bella</i>	Perennial	Native
EPBR3	<i>Epilobium brachycarpum</i>	Annual	Native
HEMI20	<i>Hemizonella minima</i>	Annual	Native
JUTE	<i>Juncus tenuis</i>	Perennial	Native
LIGL2	<i>Lithophragma glabrum</i>	Perennial	Native
LOBIL	<i>Lomatium bicolor</i> var. <i>leptocarpum</i>	Perennial	Native
LONU2	<i>Lomatium nudicaule</i>	Perennial	Native
MAGR3	<i>Madia gracilis</i>	Annual	Native
MIGR	<i>Microsteris gracilis</i>	Annual	Native
MOLI4	<i>Montia linearis</i>	Annual	Native
NAVAR	<i>Navarretia</i> sp.	Annual	Native
POAC	Unknown <i>Poaceae</i>	Perennial	Native
PODO4	<i>Polygonum douglasii</i>	Annual	Native
POPO4	<i>Polygonum polygaloides</i>	Annual	Native
POSE	<i>Poa secunda</i>	Perennial	Native
PSSP6	<i>Pseudoroegneria spicata</i>	Perennial	Native
SAAN2	<i>Sanguisorba annua</i>	Perennial	Native
SEST2	<i>Sedum stenopetalum</i>	Perennial	Native
SIID	<i>Sisyrinchium idahoense</i>	Perennial	Native
TRGR7	<i>Triteleia grandiflora</i>	Perennial	Native
TRMA3	<i>Trifolium macrocephalum</i>	Perennial	Native

TROB	<i>Trichostema oblongum</i>	Annual	Native
VEDU	<i>Ventenata dubia</i>	Annual	Introduced
ZIVE	<i>Zigadenus venenosus</i>	Perennial	Native

**Table B.4.2:** Mean trait values and standard deviations (mean; sd), the vegetation type where the species was collected, and the number of individuals collected (n) for all species included in trait analyses. Percent leaf nitrogen (leaf N %) does not have a standard deviation measurement associated with the mean because sampled leaf tissues for all individuals within each species were combined to have sufficient leaf biomass for N analysis. Species codes follow USDA Plants Database, 2020.

USDA plant code	height (cm)	specific leaf area (cm <sup>2</sup> /g)	root: shoot	root length (cm)	root diameter (mm)	fine:total root volume	leaf N (%)	collection setting	n
AGHE2	5.54; 0.97	351.5; 98.7	0.27; 0.16	22.4; 18.4	0.61; 0.29	0.89; 0.17	2.13	wet meadow	5
ALAC4	9.96; 4	84.5; 12.1	1.64; 0.25	10; 3.7	1.64; 0.46	0.13; 0.05	1.93	scab-flat	5
ALLIU	16.72; 4.16	163.5; 42.8	7.33; 4.06	14.1; 6.5	0.82; 0.14	0.13; 0.09	1.46	wet meadow	5
ANLU2	14.38; 2.99	122; 15.6	0.91; 0.21	623; 395.8	0.71; 0.13	0.36; 0.17	1.69	wet meadow	6
BRAR5	18.57; 4.51	144.7; 13.3	0.11; 0.04	39.2; 20.9	0.31; 0.03	0.62; 0.22	1.14	wet meadow	5
BRTE	10.16; 3.06	287; 98.7	0.22; 0.04	36.3; 8.6	0.36; 0.04	0.92; 0.07	0.6	low sage-steppe	5
CAQU2	22.72; 3.74	120.8; 50	8.14; 5.2	27.8; 8.3	4.83; 1.63	0.35; 0.56	1.32	wet meadow	5
CATE26	8.78; 3.26	409.5; 271.8	0.08; 0.06	7.3; 6.9	0.39; 0.08	0.95; 0.1	1.68	wet meadow	5
COPA3	4.12; 1.55	323; 144.8	0.09; 0.05	35.4; 38.6	0.28; 0.07	1; 0	1.96	wet meadow	5
DAUN	15.57; 3.47	194.2; 40.9	0.21; 0.02	1043.7; 584	0.41; 0.06	0.68; 0.24	1.18	wet meadow	5
DEDA	9.02; 2.91	208.4; 67.1	0.21; 0.14	17.0; 8.8	0.26; 0.04	1; 0	1.26	wet meadow	6
DEDI11	15.54; 2.49	245.4; 40.5	1.08; 0.37	60.7; 11.8	0.66; 0.21	0.21; 0.15	1.98	wet meadow	5
DODEC	2.64; 1.15	204; 22.9	1.45; 1.19	51.3; 16	0.52; 0.1	0.55; 0.13	1.65	wet meadow	5
ELBE	6.75; 1.87	137.5; 39.1	0.4; 0.18	34.9; 13.9	0.43; 0.07	0.46; 0.18	0.77	wet meadow	5
EPBR3	9.41; 2.49	50.1; 15	0.17; 0.04	8.7; 2.2	0.73; 0.11	0.94; 0.14	1.67	wet meadow	5
HEMI20	3.81; 1.6	136.8; 67	0.26; 0.07	3.5; 1	0.31; 0.1	1; 0	1.18	wet meadow	5
JUTE	18.26; 2.14	167.2; 124.4	0.69; 0.14	1287.1; 295.9	0.64; 0.1	0.46; 0.14	1.12	wet meadow	5
LIGL2	7.72; 2.89	234.1; 86.9	2.16; 1.42	50.4; 48.8	0.51; 0.11	0.2; 0.09	1.81	wet meadow	5
LOBIL	10.32; 1.92	82.2; 10.9	2.69; 0.94	35.3; 4	4.07; 1.72	0.01; 0.02	1.9	wet meadow	5

<b>LONU2</b>	12.57; 1.79	132; 74.8	2.00; 1.79	43.4; 16.9	4.52; 2.33	0.01; 0.01	1.62	wet meadow	5
<b>MAGR3</b>	16.44; 6.51	127; 38.1	0.15; 0.01	14.5; 3.8	0.94; 0.4	0.78; 0.32	1.42	wet meadow	5
<b>MIGR</b>	6.82; 1.79	159.5; 37	0.16; 0.09	18.0; 9.4	0.32; 0.05	1; 0	1.29	low sage- steppe	5
<b>MOLI4</b>	4.09; 0.49	133.1; 39.1	0.14; 0.1	11.8; 8.4	0.41; 0.09	0.99; 0.01	1.75	wet meadow	5
<b>NAVAR</b>	1.93; 0.61	135.8; 57.4	0.09; 0.02	4.1; 1.5	0.33; 0.09	1; 0	1.61	wet meadow	5
<b>POAC</b>	29.01; 4.59	163; 21.2	0.91; 0.48	460.6; 401.9	0.51; 0.13	0.44; 0.12	1.86	wet meadow	5
<b>PODO4</b>	7.74; 1.66	130.3; 40.1	0.14; 0.04	7.8; 2.8	0.4; 0.07	1; 0	3.26	scab-flat	5
<b>POPO4</b>	1.89; 0.38	133.3; 47.1	0.08; 0.04	3.1; 1.8	0.27; 0.04	1; 0	0.82	wet meadow	5
<b>POSE</b>	14.42; 3.58	109.5; 24.1	2.70; 1.17	1652.5; 356	0.54; 0.14	0.19; 0.1	1.36	wet meadow	5
<b>PSSP6</b>	41.21; 8.8	97.4; 58.2	3.94; 3.21	1715.6; 411.9	0.67; 0.2	0.28; 0.22	1.68	low sage- steppe	5
<b>SAAN2</b>	37.24; 7.85	131.4; 35.9	0.26; 0.09	72.3; 46.7	0.79; 0.15	0.36; 0.15	1.94	wet meadow	5
<b>SEST2</b>	11.18; 2.31	92.9; 41.3	0.12; 0.01	26.2; 8.2	0.58; 0.17	0.23; 0.11	1.23	scab-flat	5
<b>SIID</b>	18.79; 1.77	100.9; 13.7	1.76; 1.94	192.2; 189.1	0.71; 0.06	0.52; 0.1	1.94	wet meadow	5
<b>TRGR7</b>	21.25; 3.24	135.2; 33.9	4.29; 0.98	21.9; 14.2	1.41; 0.51	0.07; 0.05	1.2	wet meadow	7
<b>TRMA3</b>	5.21; 1.08	68.9; 2.3	8.97; 5.68	271.8; 86.6	1.85; 0.39	0.12; 0.06	4.18	wet meadow	5
<b>TROB</b>	3.35; 0.55	290.2; 168.3	0.14; 0.19	4.3; 2.9	0.26; 0.04	1; 0	2.12	wet meadow	5
<b>VEDU</b>	21.81; 8.12	205.0; 119.0	0.12; 0.08	7.7; 3.9	0.28; 0.02	0.98; 0.04	0.92	wet meadow	5
<b>ZIVE</b>	20.3; 2.95	132.9; 25.1	2.58; 1.73	39.9; 13.5	1.31; 0.22	0.05; 0.01	1.99	wet meadow	4

## Appendix B.5: Examining Multivariate Distance Metrics

In addition to examining *V. dubia* response to community weighted means (CWM) trait values for individual traits, we also explored how *V. dubia* responds to a multivariate distance metric including information from all measured traits. Using our community weighted mean x subplot matrix, we calculated Euclidean distance between *V. dubia* and each subplot in multidimensional CWM trait space with the package “vegan” in R (Oksanen et al. 2019). We then modeled *V. dubia* biomass (log transformed) response to Euclidean distance using a linear mixed effects model with vegetation type included as an interaction term. Random intercepts were included for plots nested within experimental blocks.

The Euclidean distance model reinforced what we found in our individual CWM trait models. As Euclidean distance increased and CWM trait values became more dissimilar to *V. dubia*'s, *V. dubia* biomass increased, but only in wet meadows (Table S1; Fig. S1). This result suggests that community trait similarity may increase invasion resistance, but only in productive vegetation types. AICc for this model was 243.2 and marginal  $r^2$  for CWM trait value Euclidean distance was 0.08.

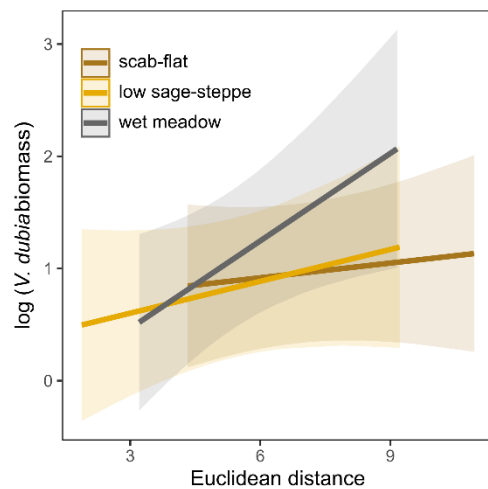
While the mean Euclidean distance did not differ between the vegetation types, subplots showed high variability in Euclidean distance values. The lowest Euclidean distance values were present in low sage-steppe subplots (Fig. S2), indicating that low-sage steppe may harbor some communities with more similar CWM trait values to *V. dubia* than the scab-flats or wet meadows. Scab-flat subplots had the highest range of Euclidean distance values (Fig. S2), indicating that these vegetation types support communities with the most dissimilar CWM trait values.

Euclidean distance explained variation in the data to the same extent as our trait metrics with the highest marginal  $r^2$  (SLA-weighted mean dissimilarity, SLA-hierarchical distance, and resident biomass). However, the predictive power of the Euclidean distance model was lower than some single trait models and the relative influence of individual traits is unclear.

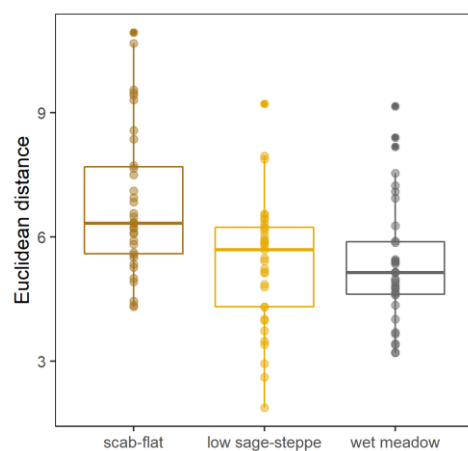


**Table B.5.1.** Slope estimates and 95% confidence intervals for CWM trait value Euclidean distance by vegetation type. Slope estimates were calculated from the package Emmeans from the full models (Russel 2021).

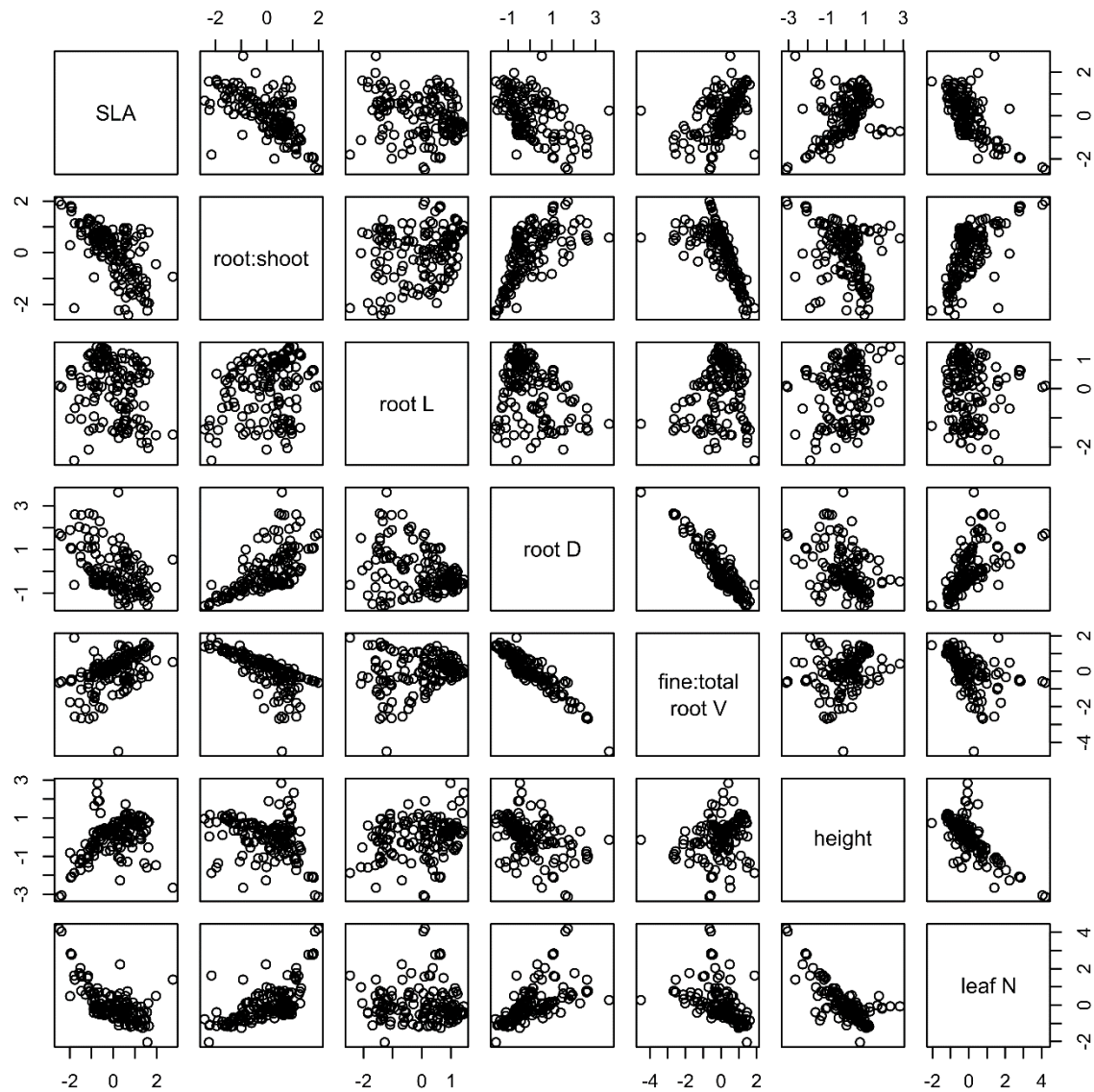
vegetation type	estimate	lower CI	upper CI
scab-flat	0.04	-0.11	0.19
low sage-steppe	0.09	-0.07	0.26
wet meadow	0.26	0.04	0.48



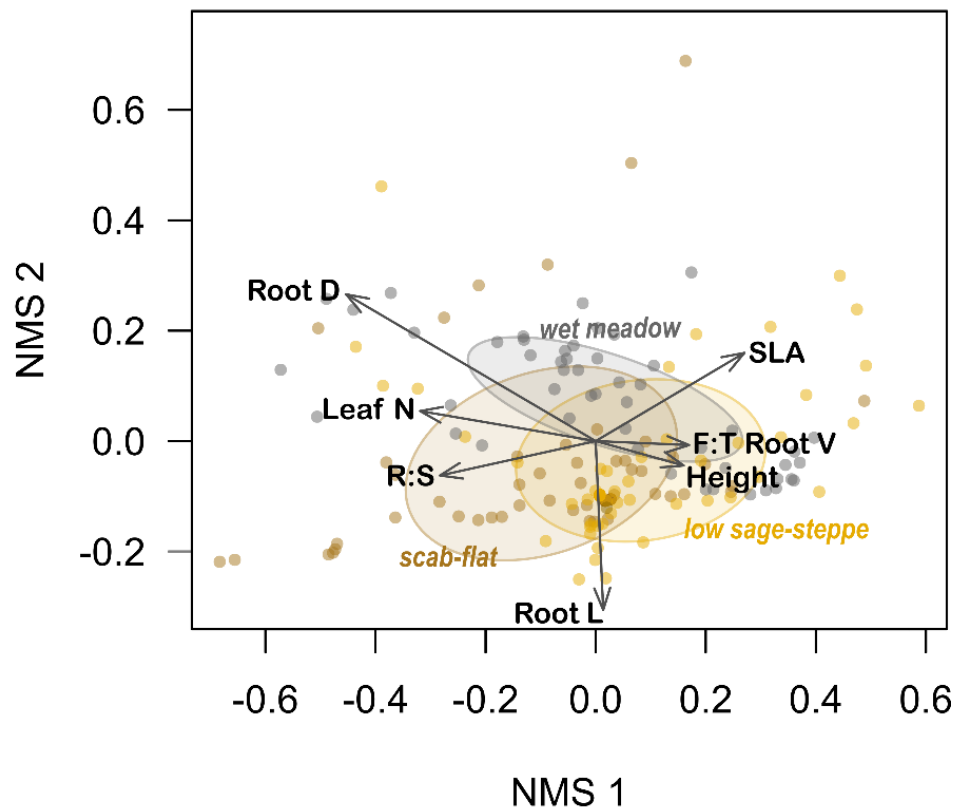
**Figure B.5.1.** *Ventemata dubia* biomass response to Euclidean distance between *V. dubia* and CWM trait values for three vegetation types situated along a vegetative productivity gradient.



**Figure B.5.2.** Euclidean distance between *V. dubia* and CWM trait values by vegetation type.



**Figure B.5.3.** Scatter plot matrix demonstrating correlations between community weighted mean trait values for each trait. SLA = specific leaf area; root:shoot = root-to-shoot ratio; root L = root length; root D = root diameter, fine:total root V = fine-to-total root volume ratio; leaf N = percent leaf nitrogen.



**Figure B.5.4.** Non-metric multidimensional scaling ordination of subplots in community-weighted mean trait space with dispersion ellipses representing the standard deviation of point scores for each vegetation type. The three vegetation types shared similar weighted mean trait values. Vectors represent linear relationships of the axes to above- and below-ground traits.

## Appendix B.6: Community metric-invasion relationships

**Table B.6.1.** AICc table with marginal  $r^2$  for every community metric model. Averaged  $r^2$  is presented for each community assembly hypothesis (shaded rows).

Model/ trait	Marginal $r^2$	AICc
<b>resident biomass</b>		
resident biomass	0.077	230.5
<b>weighted mean dissimilarity</b>		
fine:total root volume	0.073	235.3
height	0.068	233.9
leaf N	0.043	236.6
root diameter	0.046	237.8
root length	0.049	236.1
root:shoot	0.05	236.8
SLA	0.081	235.4
<b>nearest species dissimilarity</b>		
fine:total root volume	0.034	233.7
height	0.037	232.3
leaf N	0.032	232.2
root diameter	0.038	230.4
root length	0.043	234.4
root:shoot	0.026	235.5
SLA	0.035	236.4
<b>hierarchical distance</b>		
fine:total root volume	0.074	235.3
height	0.072	233.4
leaf N	0.043	236.6
root diameter	0.046	237.8
root length	0.049	236.1
root:shoot	0.05	236.8
SLA	0.081	235.6

**Table B.6.2.** Chi-squared and p-values for interaction effects between community traits and vegetation type for each community metric model. Values are reported from type III Wald chi-square tests.

<b>Model/ trait</b>	<b>Chi-sq</b>	<b>Pr. Chi-sq.</b>
<b>resident biomass</b>		
resident biomass	4.06	0.13
<b>weighted mean dissimilarity</b>		
fine:total root volume	3.78	0.15
height	2.71	0.26
leaf N	1.41	0.49
root diameter	1.5	0.47
root length	3.44	0.18
root:shoot	1.84	0.4
SLA	4.88	0.09
<b>nearest species dissimilarity</b>		
fine:total root volume	2.06	0.36
height	2.43	0.3
leaf N	1.93	0.38
root diameter	2.28	0.32
root length	1.11	0.57
root:shoot	0.21	0.9
SLA	0.98	0.61
<b>hierarchical distance</b>		
fine:total root volume	3.69	0.16
height	2.86	0.24
leaf N	1.41	0.49
root diameter	1.5	0.47
root length	3.44	0.18
root:shoot	1.84	0.4
SLA	4.95	0.08

**Table B.6.3.** Slope estimates and 95% confidence intervals for each community metric model by vegetation type. \*Indicate instances where the confidence intervals do not include zero. Slope estimates were calculated from the package Emmeans from the full models (Russel 2021).

Model/ trait	Vegetation type	Estimate	Lower CI	Upper CI
<b>resident biomass</b>				
<b>resident biomass</b>	scab-flat	-0.1	-0.35	0.14
	low sage-steppe	-0.15	-0.46	0.16
	wet meadow*	-0.56	-0.95	-0.17
<b>weighted mean dissimilarity</b>				
<b>fine:total root volume</b>	scab-flat	0	-0.28	0.28
	low sage-steppe	-0.03	-0.35	0.29
	wet meadow*	0.33	0.05	0.6
<b>height</b>	scab-flat	0.04	-0.18	0.26
	low sage-steppe	0.22	-0.1	0.53
	wet meadow*	0.38	0.01	0.75
<b>leaf N</b>	scab-flat	0.03	-0.15	0.22
	low sage-steppe	0.2	-0.26	0.67
	wet meadow	0.31	-0.17	0.8
<b>root diameter</b>	scab-flat	-0.01	-0.28	0.27
	low sage-steppe	0.02	-0.32	0.36
	wet meadow	0.23	-0.07	0.54
<b>root length</b>	scab-flat	0.25	-0.05	0.56
	low sage-steppe	0.04	-0.21	0.3
	wet meadow	-0.2	-0.57	0.17
<b>root:shoot</b>	scab-flat	0.2	-0.05	0.45
	low sage-steppe	-0.03	-0.29	0.23
	wet meadow	0.18	-0.19	0.56
<b>SLA</b>	scab-flat	-0.02	-0.25	0.21
	low sage-steppe	-0.03	-0.29	0.24
	wet meadow*	0.44	0.06	0.82
<b>nearest species dissimilarity</b>				
<b>fine:total root volume</b>	scab-flat	-0.03	-0.35	0.29
	low sage-steppe	-0.38	-0.9	0.13
	wet meadow	0.33	-0.69	1.35
<b>height</b>	scab-flat	-0.1	-0.66	0.46
	low sage-steppe	-0.32	-1.08	0.43
	wet meadow	0.56	-0.32	1.43
<b>leaf N</b>	scab-flat	0.04	-0.56	0.64

	low sage-steppe	-0.47	-1.24	0.29
	wet meadow	0.35	-0.67	1.38
<b>root diameter</b>	scab-flat	-0.06	-0.52	0.4
	low sage-steppe	-0.23	-0.94	0.47
	wet meadow	-1.74	-3.93	0.45
<b>root length</b>	scab-flat	-0.04	-0.37	0.28
	low sage-steppe	-0.28	-0.57	0.02
	wet meadow	-0.19	-0.79	0.42
<b>root:shoot</b>	scab-flat	-0.07	-0.39	0.24
	low sage-steppe	-0.16	-0.68	0.36
	wet meadow	-0.28	-1.22	0.66
<b>SLA</b>	scab-flat	-0.01	-0.38	0.37
	low sage-steppe	0.07	-0.32	0.46
	wet meadow	0.31	-0.21	0.83
<b>hierarchical distance</b>				
<b>fine:total root volume</b>	scab-flat	-0.01	-0.28	0.26
	low sage-steppe	0.03	-0.29	0.35
	wet meadow*	-0.33	-0.6	-0.05
<b>height</b>	scab-flat	-0.04	-0.26	0.18
	low sage-steppe	-0.24	-0.53	0.06
	wet meadow*	-0.38	-0.75	-0.01
<b>leaf N</b>	scab-flat	0.03	-0.15	0.22
	low sage-steppe	0.2	-0.26	0.67
	wet meadow	0.31	-0.17	0.8
<b>root diameter</b>	scab-flat	-0.01	-0.28	0.27
	low sage-steppe	0.02	-0.32	0.36
	wet meadow	0.23	-0.07	0.54
<b>root length</b>	scab-flat	0.25	-0.05	0.56
	low sage-steppe	0.04	-0.21	0.3
	wet meadow	-0.2	-0.57	0.17
<b>root:shoot</b>	scab-flat	0.2	-0.05	0.45
	low sage-steppe	-0.03	-0.29	0.23
	wet meadow	0.18	-0.19	0.56
<b>SLA</b>	scab-flat	0.02	-0.19	0.22
	low sage-steppe	0.03	-0.24	0.29
	wet meadow*	-0.44	-0.82	-0.06

## Appendix C Supplementary material for Chapter 4

### Appendix C.1: Vegetation type classifications (modified from LANDFIRE Existing Vegetation Type 2.0.0)

SAF_SRM	EVT_CLASS	Reclassified Veg. Type
LF 11: Water	Non-vegetated	Non-vegetated
LF 12: Snow-Ice	Non-vegetated	Non-vegetated
LF 33: Sparsely Vegetated	Sparsely vegetated	Sparsely vegetated
LF 41: Deciduous Shrubland	Shrubland	Shrubland
LF 52: Introduced Upland Vegetation - Shrub	Shrubland	Shrubland
LF 54: Introduced Upland Vegetation - Herbaceous	Herbaceous - grassland	Herbaceous/Grassland
LF 56: Western Herbaceous Wetland	Herbaceous - grassland	Wetland/Riparian
LF 58: Introduced Woody Wetlands and Riparian Vegetation	Herbaceous - grassland	Wetland/Riparian
LF 59: Introduced Herbaceous Wetland and Riparian Vegetation	Herbaceous - grassland	Wetland/Riparian
LF 62: Recently Logged - Herbaceous	Herbaceous - grassland	Recently Disturbed
LF 63: Recently Logged - Shrub	Shrubland	Recently Disturbed
LF 64: Recently Logged - Tree	Open tree canopy	Recently Disturbed
LF 66: Recently Burned - Herbaceous	Herbaceous - grassland	Recently Disturbed
LF 67: Recently Burned - Shrub	Shrubland	Recently Disturbed
LF 68: Recently Burned - Tree	Open tree canopy	Recently Disturbed
LF 80: Agriculture	Herbaceous - grassland	Agriculture
LF 80: Agriculture	Open tree canopy	Agriculture
LF 98: Recently Disturbed Other - Herbaceous	Herbaceous - grassland	Recently Disturbed
LF 99: Recently Disturbed Other - Shrub	Shrubland	Recently Disturbed
LF 100: Recently Disturbed Other - Tree	Open tree canopy	Recently Disturbed
SAF 206: Engelmann Spruce-Subalpine Fir	Closed tree canopy	Closed tree canopy
SAF 208: Whitebark Pine	Open tree canopy	Open tree canopy
SAF 209: Bristlecone Pine	Open tree canopy	Open tree canopy
SAF 210: Interior Douglas-Fir	Closed tree canopy	Closed tree canopy
SAF 212: Western Larch	Open tree canopy	Open tree canopy
SAF 213: Grand Fir	Closed tree canopy	Closed tree canopy
SAF 217: Aspen	Open tree canopy	Open tree canopy
SAF 218: Lodgepole Pine	Closed tree canopy	Closed tree canopy
SAF 227: Western Redcedar-Western Hemlock	Closed tree canopy	Closed tree canopy
SAF 235: Cottonwood-Willow	Open tree canopy	Open tree canopy



SAF 237: Interior Ponderosa Pine	Open tree canopy	Open tree canopy
SRM 101: Bluebunch Wheatgrass	Herbaceous - grassland	Herbaceous/Grassland
SRM 106: Bluegrass Scabland	Dwarf-shrubland	Dwarf-shrubland
SRM 106: Bluegrass Scabland	Herbaceous - shrub-steppe	Dwarf-shrubland
SRM 107: Western Juniper-Big Sagebrush-Bluebunch Wheatgrass	Open tree canopy	Open tree canopy
SRM 109: Ponderosa Pine-Shrubland	Sparse tree canopy	Open tree canopy
SRM 311: Rough Fescue-Bluebunch Wheatgrass	Herbaceous - grassland	Herbaceous/Grassland
SRM 312: Rough Fescue-Idaho Fescue	Herbaceous - grassland	Herbaceous/Grassland
SRM 314: Big Sagebrush-Bluebunch Wheatgrass	Herbaceous - shrub-steppe	Shrub-steppe
SRM 402: Mountain Big Sagebrush	Herbaceous - shrub-steppe	Shrub-steppe
SRM 403: Wyoming Big Sagebrush	Herbaceous - shrub-steppe	Shrubland
SRM 403: Wyoming Big Sagebrush	Shrubland	Shrubland
SRM 406: Low Sagebrush	Herbaceous - shrub-steppe	Dwarf-shrubland
SRM 409: Tall Forb	Herbaceous - grassland	Herbaceous/Grassland
SRM 410: Alpine Rangeland	Dwarf-shrubland	Herbaceous/Grassland
SRM 410: Alpine Rangeland	Herbaceous - grassland	Herbaceous/Grassland
SRM 415: Curlleaf Mountain-Mahogany	Open tree canopy	Open tree canopy
SRM 421: Chokecherry-Serviceberry-Rose	Shrubland	Shrubland
SRM 422: Riparian	Herbaceous - grassland	Wetland/Riparian
SRM 422: Riparian	Shrubland	Wetland/Riparian
SRM 501: Saltbush-Greasewood	Shrubland	Shrubland

Non-burnable and non-vegetated areas (e.g. urban areas, snow/ice, open water, and agriculture managed in a non-burnable condition) were removed from the dataset prior to all analysis as they have insufficient fuels to carry wildfires under any condition.

## **Appendix C.2 Vegetation codes included in core *ventenata* habitat low-productivity vegetation layer and additional methods.**

To create the most accurate low-productivity core habitat layer possible given existing vegetation mapping efforts, we combined spatial layers from three sources available at different scales and extents: USDA National Forest Potential Vegetation Type (PVT) (Hall 1998) (Table S1), Simpson’s PVT for Oregon (Simpson 2019), and LANDFIRE Existing Vegetation Type (EVT) for the study region (LANDFIRE 2019a). According to local experts, the National Forest and Simpson’s vegetation layers provide a more detailed representation of non-forested vegetation than LANDFIRE vegetation layers within the ecoregion, but these layers were not available for the entire Blue Mountain Ecoregion. For representation across the ecoregion, we cross-walked the US Forest Service and Simpson’s vegetation layers with LANDFIRE and selected the LANDFIRE EVTs that had the greatest overlap to include in the layer. Simpson’s PVTs included in core habitat layer were “scabland shrub”, “scabland grass”, and “juniper steppe”. LANDFIRE EVTs included in the core habitat layer were “Columbia Plateau Steppe and Grassland”, “Columbia Plateau Scabland Shrubland”, and “Columbia Plateau Low Sagebrush Steppe”.

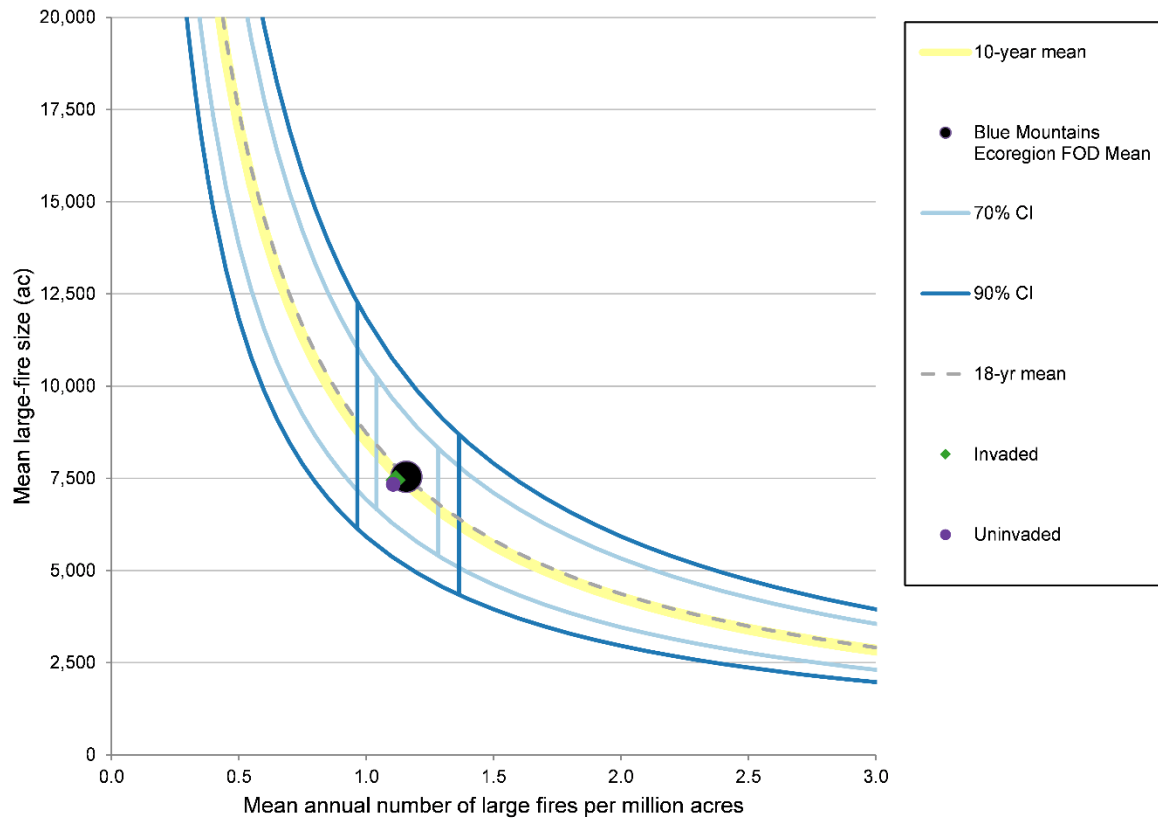
To isolate the effects of the *ventenata* invasion from other annual grass invasions, we excluded big sagebrush (*Artemisia tridentata*) potential vegetation types (Hall 1998, Simpson 2019) which were common along the edges of the study region, because these areas were more likely to have been invaded by cheatgrass prior to the *ventenata* invasion (Bradley et al. 2017). Alpine and subalpine areas were not included because they are not known to be at high risk for *ventenata* invasion at this time (Tortorelli et al. 2020, Nietupski 2021). All vegetation types included in the vegetation layer were determined through discussions with ecologists, botanists, and weed managers as well as vegetation map product developers.

**Table C.2.1.** FSVeg Potential vegetation codes included in low-productivity vegetation layer

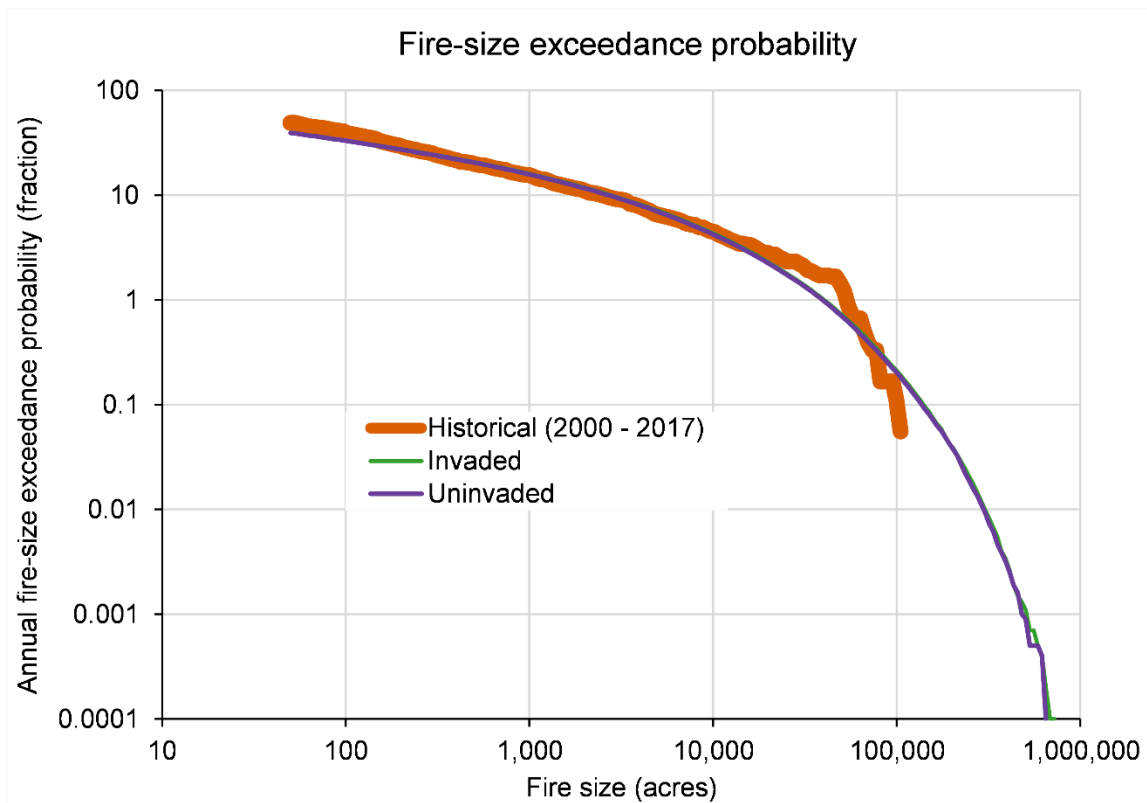
<b>Ecoclass code</b>	<b>Vegetation Association</b>	<b>Series</b>	<b>herbage (lb/acre)</b>
CJS111	JUOC/ARAR/AGSP-FEID	western juniper	411
CJS111	JUOC/AGSP-FEID	western juniper	363
CJS112	JUOC/ARAR/FEID	western juniper	350
CJS811	JUOC/ARRI/POSA3	western juniper	207
FM9111	ERDO/POSA3	buckwheat	315
FM9112	ERST2/POSA3	buckwheat	118
FM9113	ERUM-RIDGE	buckwheat	40
FM9911	ERLA-PHHE	Eriophyllum	150
FX4111	LECOW-RIM	Wallowa lewisia	25
GB1911	AGSP-SPCR-ARLO3	bluebunch wheatgrass	655
GB20	STOC-POSA3	needlegrass	
GB21	STOC-POSA3-ERNI	needlegrass	
GB4111	AGSP/ERHE	bluebunch wheatgrass	420
GB4112	AGSP/POSA3/SCAN	bluebunch wheatgrass	385
GB4113	AGSP/POS3-BASALT	bluebunch wheatgrass	685
GB4114	AGSP-/POSA3/ASCU4	bluebunch wheatgrass	420
GB4115	AGSP/POSA3/ERPU	bluebunch wheatgrass	665
GB4116	AGSP/POSA3-GRANITE	bluebunch wheatgrass	550
GB4118	AGSP/POSA3/OPPO	bluebunch wheatgrass	380
GB4122	AGSP-FEID	bluebunch wheatgrass	787
GB4911	AGSP-POSA3-DAUN	bluebunch wheatgrass	
GB4912	AGSP/POSA3-SHAL/STEEP	bluebunch wheatgrass	679
GB4913	AGSP/POSA3-SHAL/STEEP	bluebunch wheatgrass	300
GB4914	AGSP-FEID-DEEP/STEEP	bluebunch wheatgrass	434
GB9111	POSA3-DAUN	sandberg's bluegrass	160
GB99	POSA3-FEMI	sandberg's bluegrass	70
GBRX	Bunchgrass; rocky, steep, rough		
NRS0	rocky land with scattered shrubs or brush		
SD19-		low sagebrush	
SD1911	ARAR/AGSP-FEID	low sagebrush	411
SD1912	ARAR/FEID/POSA3	low sagebrush	179
SD1913	ARAR/FEID/SIHY	low sagebrush	245
SD9111	ARRI/POSA3-SCAB	rigid sagebrush	207
SD9131	ARRI/POSA3-LOMA	rigid sagebrush	225
SD9211	ARAR/POSA3-HAST	low sagebrush	150
SD9212	ARAR/POSA3-DAUN	low sagebrush	125
SD9221	ARAR/POSA3	low sagebrush	181
SD9322	ERMI-PHOR	buckwheat	26

SD9323	ERUM/STIPA-PUM	buckwheat	10
SDB9	Buscuit-scabland complex, sagebrush		

### Appendix C.3 FSim simulation calibration



**Figure C.3.1.** FSim simulation calibration targets and results of FSim simulations. Simulations were calibrated to historical measures of large fire occurrence including mean historical large-fire size, mean annual burn probability, mean annual number of large fires per million acres, and mean annual area burned per million acres. From these measures, two calculations are particularly useful for comparing against and adjusting FSim results: 1) mean large fire size, and 2) number of large fires per million acres. All runs were completed at 120-m resolution with 10,000 iterations. FOD = fire occurrence dataset (here, 2000 to present).



**Figure C.3.2.** Fire-size exceedance probability for completed FSim simulations. Care was taken to match simulated wildfire size distributions to the historical record and allow for the occurrence of simulated fires larger than any observed historically. While only large-fire sizes >247 acres (100 ha) were used to establish calibration targets, numerous small fires were also simulated. The impact of small fires on landscape burn probability is generally negligible.

**Appendix S4. Total hectares burned per year by vegetation type according to the vegetation type where each ignition occurred for the uninvaded and invaded simulations (uninvaded; invaded).**

<b><u>Ignition Vegetation type</u></b>	<b><u>Affected Vegetation type</u></b>							
	Agriculture e/ Wetland	Closed tree canopy	Dwarf- shrubland	Herbaceous / Grassland	Open tree canopy	Recently disturbed	Shrubland	Sparsely vegetated
Agriculture /Wetland	128; 129	222; 224	48; 55	85; 88	122; 127	7; 7	233; 239	5; 5
Closed tree canopy	435; 444	17,833; 17,890	471; 549	1487; 1517	4,220; 4,327	380; 382	1,865; 1,928	208; 207
Dwarf- shrubland	53; 59	298; 343	349; 454	230; 256	470; 545	25; 28	811; 879	13; 14
Herbaceous /Grassland	95; 97	899; 922	238; 263	1,348; 1,372	474; 498	96; 98	1,007; 1,025	55; 55
Open tree canopy	236; 248	3,822; 3,907	666; 800	689; 724	3,787; 3,966	144; 151	2,320; 2,426	72; 73
Recently disturbed	14; 14	344; 342	42; 46	160; 161	171; 176	83; 84	205; 208	15; 15
Shrubland	265; 270	1,101; 1,120	792; 862	1,034; 1,058	1,764; 1,828	119; 123	4,753; 4,823	87; 88
Sparsely vegetated	3; 3	84; 84	10; 10	39; 40	40; 41	5; 5	61; 62	7; 7

### Appendix C.5. GAM summary statistics for spatial patterns of invasion models

All models were fit with a single predictor and a Gaussian distribution.

Model	EDF (k' = 9)	Deviance	Dispersion	R <sup>2</sup> (adj.)	GCV score
<b>focal forest ~ proportion neighborhood invaded</b> (n = 357,182)					
Annual burn probability					
difference (invaded - uninvaded)	6.87	0.4	0	0.248	0
invaded	5.89	8.5	0	0.002	0
uninvaded	6.10	8.0	0	0.028	0
Conditional burn probability >1.2m					
difference (invaded - uninvaded)	6.48	1978.2	0.006	0.066	0.006
invaded	5.22	30821.0	0.086	0.004	0.086
uninvaded	5.58	31117.4	0.087	0	0.087
Conditional burn probability >2.4m					
difference (invaded - uninvaded)	6.85	629.7	0.002	0.020	0.002
invaded	6.64	9426.6	0.026	0.005	0.026
uninvaded	6.58	9050.5	0.025	0.010	0.025
<b>Patch ~ log(patch area)</b> (n = 17,783)					
Annual burn probability					
difference (invaded - uninvaded)	3.78	0.0	0	0.035	0
invaded	3.91	0.4	0	0	0
uninvaded	2.72	0.4	0	0.004	0
Conditional burn probability >1.2m					
difference (invaded - uninvaded)	1.63	922.1	0.052	0.007	0.052
invaded	1.90	451.3	0.025	0.022	0.025
uninvaded	1.00	1350.3	0.076	0	0.076
<b>landscape ~ proportion landscape invaded</b> (n = 789,062)					



Annual burn probability					
difference (invaded - uninvasion)	8.97	0.9	0	0.424	0
invaded	8.68	17.6	0	0.004	0
uninvaded	7.54	15.3	0	0.048	0
Conditional burn probability >1.2m					
difference (invaded - uninvasion)	8.98	1176.1	0.001	0.778	0.001
invaded	6.69	12959.1	0.016	0.192	0.016
uninvaded	8.80	14567.0	0.018	0.005	0.018
Conditional burn probability >2.4m					
difference (invaded - uninvasion)	8.99	178.6	0	0.373	0
invaded	8.96	2213.0	0.003	0.032	0.003
uninvaded	8.47	2174.9	0.003	0.076	0.003